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Nr. 97

THE DOWNTONIAN AND DEVONIAN VERTEBRATES OF SPITSBERGEN. IX

MORPHOLOGIC AND SYSTEMATIC STUDIES OF THE SPITSBERGEN CEPHALASPIDS

RESULTS OF TH. VOGT'S EXPEDITION 1928
AND THE ENGLISH-NORWEGIAN-SWEDISH EXPEDITION 1939

BY

GUSTAV WÄNGSJÖ

WITH 108 FIGURES IN THE TEXT AND 118 PLATES

A. TEXT

OSLO
I KOMMISJON HOS JACOB DYBWAD
1952

NORSK POLARINSTITUTT
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Observatoriegaten 1, Oslo

SKRIFTER

Resultater av De Norske statsunderstøttede Spitsbergenekspeditioner.

Nr. 1. Hoel, A., *The Norwegian Svalbard Expeditions 1906—1926.* 1929. Kr. 10,00.
„ 2. Ravn, J. P. J., *On the Mollusca of the Tertiary of Spitsbergen.* 1922. Kr. 1,60.
„ 3. Werenskiold, W. and I. Oftedal, *A burning Coal Seam at Mt. Pyramide, Spitsbergen.* 1922. Kr. 1,20.
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„ 5. Lynge, B., *Lichens from Spitsbergen.* 1924. Kr. 2,50.
„ 6. Hoel, A., *The Coal Deposits and Coal Mining of Svalbard.* 1925. Kr. 10,00. [Out of print.]
„ 7. Dahl, K., *Contributions to the Biology of the Spitsbergen Char.* 1926. Kr. 1,00.
„ 8. Holtedahl, O., *Notes on the Geology of Northwestern Spitsbergen.* 1926. Kr. 5,50.
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„ 10. Iversen, T., *Hopen (Hope Island), Svalbard.* 1926. Kr. 7,50.
„ 11. Quenstedt, W., *Mollusken a. d. Redbay- u. Greyhookschichten Spitzb.* 1926. Kr. 8,50.
„ 1—11: Vol. I. From Nr. 12 the papers are only numbered consecutively.

Skrifter om Svalbard og Nordishavet.

Nr. 12. Stensiö, E. A:son, *The Downtonian and Devonian Vertebrates of Spitsbergen.* Part I. *Cephalaspidae.* A. Text, and B. Plates. 1927. Kr. 60,00.

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Nr. 13. Lind, J., *The Micromycetes of Svalbard.* 1928. Kr. 6,00.
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„ 18. Hoel, A. und A. K. Orvin, *Das Festungsprofil auf Spitzbergen. Karbon-Kreide.* I. Vermessungsresultate. 1937. Kr. 4,00.
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„ 22. Heintz, A., *Die Downtonischen und Devonischen Vertebraten von Spitzbergen.* II. *Acanthaspida.* 1929. Kr. 15,00.
„ 23. Heintz, A., *Die Downtonischen und Devonischen Vertebraten von Spitzbergen.* III. *Acanthaspida. — Nachtrag.* 1929. Kr. 3,00.
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„ 30. Orvin, A. K., *Beiträge zur Kenntnis des Oberdevons Ost-Grönlands.* Heintz, A., *Oberdevonische Fischreste aus Ost-Grönland.* 1930. Kr. 4,00.
„ 31. Frebold, H., *Verbr. und Ausb. des Mesozoikums in Spitzbergen.* 1930. Kr. 17,00.
„ 32. Abs, O., *Über Epidemien von unspezifischen Katarrhen der Luftwege auf Svalbard.* 1930. Kr. 2,00.
„ 33. Kiær, J., *Ctenaspis, a New Genus of Cyathaspidian Fishes.* 1930. Kr. 1,00.
„ 34. Tolmatchew, A., *Die Gattung Cerastium in der Flora von Spitzbergen.* 1930. Kr. 1,00.

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EMIL MOESTUE A/S BOKTRYKKERI

Contents.

In publications issued by Norsk Polarinstitutt the place-names of Svalbard are generally given in the recognized Norwegian forms. However, in this publication the English forms appear because the author had used them and because we, owing to various circumstances, had no opportunity to examine the paper before we received the page proofs.

NORSK POLARINSTITUTT

Preface.

During the geological investigations in Spitsbergen carried out by the Norwegian expeditions in the years of 1906—1925 inter alia a large material of Devonian vertebrates was brought together. Of this material the Cephalaspids have been described by Stensiö in 1927, whereas some other groups have been treated by Kiær and Heintz (in 1929, 1930, 1932, 1935 and 1937).

Since 1925 large new collections of fossil vertebrates have been made in the Devonian of Spitsbergen by Th. Vogt's expedition in 1928 (see Vogt 1930) and by a special palaeontological English-Norwegian-Swedish expedition in 1939, here briefly called the ENS expedition.

The present work is devoted to the Cephalaspids in the said new collections.

The greater and most important part of this new material of Cephalaspids was brought home by the ENS expedition. The planning and realization of this expedition was mainly the work of Professor E. Stensiö, Stockholm, under whose leadership the expedition was carried out. Otherwise the expedition was the result of a close cooperation between the British Museum of Natural History in London, the Palaeontological Museum in Oslo and the Palaeozoological Department of the Swedish Museum of Natural History in Stockholm, and as leaders from the English and Norwegian sides took part Dr. E. I. White, London, and Professor A. Heintz, Oslo. An account of the expedition and of the geological results, obtained during it, has been published by Føyn and Heintz (1943). The expedition visited most of the Devonian areas both in the Ice Fiord district and at the firths of the north coast. Particularly the Wood Bay series yielded much material, and its vertebrate fauna appeared to be surprisingly rich both in Cephalaspids and other lower vertebrates. A large and important material of lower vertebrates was also collected in the Red Bay series. In all more than 600 specimens of Cephalaspids were brought back by the expedition.

The material of Cephalaspids brought home by Th. Vogt's expedition in 1928 mostly comes from the Red Bay series. It includes 132 specimens, several of which are excellently preserved and very valuable from an anatomical point of view.

Besides the collections just mentioned some previously undescribed specimens from Th. Vogt's expedition in 1925 (see Vogt 1926) and a single specimen of the Lewin collection in the Palaeozoological Department of the Swedish Museum of Natural History in Stockholm have also been dealt with in the present work.

The writer has had the opportunity of going through all the specimens of Cephalaspids described by Stensiö and some of these specimens are also treated and discussed in the present work.

The material of Cephalaspids collected by the Norwegian expeditions in 1906—1928 all is in the possession of the Palaeontological Museum of Oslo. It will be referred to below under the numbers of that museum. The material of Cephalaspids brought together by the ENS expedition belongs to the British Museum (N. H.) in London, the Palaeontological Museum in Oslo and the Palaeozoological Department of the Swedish Museum of Natural History in Stockholm, but as it has not yet been divided among these museums, it will here be dealt with as a unit so that the individual specimens are referred to as ENS nos. 1—616, respectively.

In view of the circumstance that Stensiö's paper is chiefly a treatise of the anatomy of the Cephalaspids, the present work was originally planned as a taxonomic research of the new material of Spitsbergen Cephalaspids collected since 1925. During the course of the investigations it appeared, however, that the material also offers much of anatomical interest. Under such conditions it was necessarry to treat here some points of the general morphology, and hence the present work also includes an anatomic part. This part does not contain a complete account of the anatomy, but intends chiefly to point out certain new facts and to describe such structures which are of general interest and lead to new interpretations of certain anatomical conditions.

In presenting the results of my investigations I wish first to express my great obligation to Professor E. Stensiö, Stockholm, Dr. E. I. White, London, and Professor A. Heintz, Oslo, for entrusting to me this valuable material. I also acknowledge here my debt of gratitude to the late Professor G. Säve-Söderbergh for excellent working facilities at the Palaeontological Institute of Uppsala. To Dr. Elsa Warburg and Professor P. Thorslund, the succeding heads of the institute, I also wish to express my grateful thanks. For their efforts of bringing this paper into press I tender my sincere thanks to Professor A. Heintz, Oslo, and to Professor H. U. Sverdrup, Director of Norsk Polarinstitutt, Oslo.

The retouching of the photographs and the final drawings of the figures have been made by Messrs. E. Ståhl and A. Nilsson, Uppsala; a few photographs have been retouched by Mr. S. Ekblom, Stockholm. The revision of the English manuscript has been made by Professor O. Zdansky, Uppsala. To these collaborators and to others who in any way have facilitated my work I here wish to express my cordial thanks.

Introduction.

The magnificent monograph by Stensiö (1927) on the Cephalaspids from Spitsbergen constitutes a milestone in the history of investigations into the Osteostraci and likewise all other sections of fossil agnathous vertebrates, and it forms the natural and, in fact, only conceivable basis for all subsequent works on this group.

Through the researches of Stensiö our knowledge of the most primitive fossil vertebrates was immediately enormously enlarged. The inner anatomical structure of the cephalic shield in the Osteostraci was elucidated in detail, and it was thereby made wholly evident that the group belongs to the agnathous and monorhinous vertebrates. The relation of the Osteostraci to the other groups of the Ostracoderms and to the recent Cyclostomes was discussed. The group was proved to be most nearly related to the Anaspida, and it was thought to be more closely akin to one of the two recent cyclostomous groups, viz. the Petromyzonts, than these between themselves. A later paper by Stensiö (1932), on the Cephalaspids of Great Britain, supplements this work in dealing particularly with the trunk behind the cephalic shield and the minute structure of the exoskeleton.

A valuable abstract of the results of Stensiö on the cephalic anatomy of the Cephalaspids is given in a paper by Stensiö & Holmgren (1936) which also contains many comparisons with the modern Cyclostomes.

Stensiö's conclusions with regard to the Osteostraci as agnathous vertebrates have been generally accepted but in reference to the contents of the group Ostracoderms and to the interrelationship between its different sub-groups and between these and the two recent cyclostomous groups, the opinions of later authors are much at variance.

Following upon the works of Stensiö our knowledge of the Osteostraci has been increased by the researches of several authors.

The Osteostraci faunas of Saaremaa (Oesel; cf. also Luha 1940; Bölau 1949; Robertson 1951a), most interesting in view of being the oldest well preserved vertebrate faunas known dating from the Lower Ludlow, have been the subject of extensive researches. A very large material was brought home by Patten, and he has briefly described (Patten 1931) two new species of *Tremataspis (T. milleri* and *T. mam-*

millata) and *"Didymaspis" pustulata* as well as a new genus *Dartmuthia,* with the species *D. gemmifera,* considered to represent a new family connecting the Cephalaspids with the Tremataspids. A new restoration of the lower side of the shield in *Tremataspis,* showing the disposition of the plates of the oralo-branchial fenestra, was also given by Patten (1932).

After the death of Patten in 1932 his material has been worked up by Robertson in a long series of papers. The genus *Dartmuthia* was more fully described and figured (Robertson 1935a), a new genus, *Oeselaspis,* was founded (Robertson 1935b) on *"Didymaspis" pustulata* and a detailed description was given of the species. In the same year he gave a preliminary classification of the Osteostraci (Robertson 1935c) as follows:

> "Family Cephalaspidae Agassiz 1844
>   Sub-family Cephalaspinae Stensiö 1932
>   Sub-family Kiaeraspinae Stensiö 1932
> Family Trematsapidae Woodward 1891
> Family Dartmuthiidae Patten 1931
> Family Oeselaspidae Robertson 1935."

Robertson (1938a) has furthermore dealt with the Tremataspids. He gives i. a. a new restoration of the plates of the oralo-branchial fenestra, and a description of the courses of the sensory lines and of some details of the inner anatomy; seven species of the genus are described (four of them as new species, viz. *T. panderi, T. patteni, T. rohoni* and *T. scalaris;* cf. Luha 1940; Denison 1947).

Two new genera have been proposed by Robertson (1938b): *Saaremaaspis,* supposedly with short cornua and with one pair of short lateral sensory fields, is assumed to belong to the sub-family "Kiaeraspinae"; type species (and only species) is *Tremataspis mickwitzi* of Rohon (1892). *Rotsiküllaspis* with the new species *R. obrutchevi* is apparently related to *Dartmuthia.*

In a later paper (Robertson 1939a) he redescribes the species *Cephalaspis schrenkii,* erected by Pander as early as in 1856, and proposes the new genus *Witaaspis* for its reception.

A supposed representative of the genus *Cephalaspis* from Saaremaa is described (Robertson 1939b) as *C. oeselensis* in a paper which also contains a survey of the Osteostraci from Saaremaa, described till then. *Rotsiküllaspis* is now assigned to the family Dartmuthiidae. A second species of *Witaaspis (W. patteni)* is described (Robertson 1940a). A description of the sensory lines in *Thyestes verrucosus* is given in the same year (Robertson 1940b), and these lines are found in some respects to agree with those of *Tremataspis.*

In 1945 Robertson (1945) gives a redescription of the Saaremaa species placed by him in the family "Cephalaspidae", viz. *Thyestes* *verrucosus, Witaaspis schrenkii, W. patteni, Saaremaaspis mickwitzi* and *Cephalaspis oeselensis.* He also discusses all the genera proposed in this family, and the characteristics which are thought to denote groups of family rank, and, finally, gives a classification list of all the genera in Osteostraci. His list, down to sub-families, runs as follows:

> "Order Osteostraci Lankester
> Family Cephalaspidae Agassiz
> Sub-family Cephalaspinae Stensiö
> Sub-family Hemicyclaspinae Heintz
> Sub-family Kiaeraspinae Stensiö
> Family Tremataspidae Woodward
> Family Dartmuthiidae Patten
> Family Oeselaspidae Robertson
> Family Didymaspidae n. fam."

It is a development of his list in 1935, and it is interesting to note that the order is not subdivided into groups of super-family rank (the Tremataspids are thus not placed in a group distinct from the other families, cf. Berg 1937; 1940; Heintz 1939) and that the genus *Didymaspis* is placed in a family of its own.

The minute structure of the exoskeleton of *Tremataspis* and other Silurian Osteostraci has been studied by Gross (1935; 1947), Wängsjö (1944), Bölau (1951), and particularly by Denison (1947; 1951b); the latter, and Bölau, have observed the relations of the sensory lines to the mucous canals, and have both put forward a new interpretation of this canal system; they have also made some very interesting observations on the growth of the exoskeleton. Denison's interpretation of the mucous canal system has rightly been critizised by Robertson in a recent paper (Robertson 1950), in which he also enters upon a discussion of the specific criteria used in the Cephalaspids and more especially in the genus *Tremataspis.*

Four new *Cephalaspis* species *(C. canadensis, C. acadica* from the supposed Eodevonian, and *C. patteni, C. rosamundae* from the Neodevonian) from Canada have been described by Robertson (1936; 1937; 1941).

The first Cephalaspid, found in U.S.A., has been described by Bryant (1933) as *Cephalaspis wyomingensis.* Some very small bone fragments *(Ohioaspis)* from the Mesodevonian of Ohio have been referred to Osteostraci on account of their minute structure (Wells 1944).

In Germany som badly preserved remains are described as *Cephalaspis diensti,* in addition to two indeterminable Cephalaspid fragments, all from the Upper Eodevonian (Gross 1933a; 1933b; 1937).

A partly exceptionally well preserved specimen, holotype for the new species *Cephalaspis kozlowskii,* has been thoroughly studied by

Zych (1937); some of the superficial vascular canals of the dorsal side of the shoulder-girdle are described and interpreted as being connected to the vascular canal system of the pectoral fin, and the n. glossopharyngeus is said to have run in a canal behind the labyrinth cavity and not to have pierced this cavity.

A new *Cephalaspis* species *(C. jacki)* is described from England by White (1935b) and a new *Benneviaspis* species *(B. longicornis)* from Spitsbergen by Wängsjö (1937).

A badly preserved specimen and some isolated scales from the Downtonian of Scotland are described as a new genus and species, *Hemiteleaspis heintzi,* by Westoll (1945), who in this connection also enters upon several questions of general interest with regard to the anatomy and growth of the cephalic shield and the evolution of the Osteostraci.

Lehman (1937) has described undeterminable fragments of Osteostraci from the Upper Ludlow of Scania (Sweden), and some fragments (i. a. of *Darthmuthia)* from Gotland are mentioned by Spjeldnæs (1950).

In a most important paper Heintz (1939) has given a very detailed account of two Cephalaspids from the Downtonian of Norway, viz. *Aceraspis robusta* and *Hirella ("Micraspis") gracilis,* first described by Kiær (1911). He gives i. a. interesting informations on the sclerotic ossifications and on the ventral visceral exoskeleton, and according to him, the position and the shape of the mouth opening is quite different in these two closely related forms. Both species have the anterior portion of the dorsal fin-fold developed as a high and thin anterior dorsal fin or fin-like crest (it is, however, interpreted as being formed in essentially the same way as the dorsal crest in e. g. *Hemicyclaspis).* Very peculiar is the structure of the caudal fin with a horizontal membrane on its antero-ventral part (this membrane is shown to occur also in *Hemicyclaspis, Ateleaspis* and *Cephalaspis,* and is thought to be characteristic of the caudal fin of the Cephalaspids in general). *Ateleaspis tesselata* is also redescribed. This genus, and *Aceraspis, Hirella* and *Hemicyclaspis* are placed in a subfamily of their own, "Hemicyclaspinae". The classification of the order Osteostraci according to Heintz is this:

"Order Osteostraci
    Sub-order Cephalaspida
        Fam. Cephalaspidae
            Sub-Fam. Hemicyclaspinae

            . . . .

            Sub-Fam. Cephalaspinae

            . . . .

        Fam. Kiaeraspidae
    Sub-order Tremataspida."

Recently Denison (1951a), in a paper on the evolution and classification of the Osteostraci has put forward a new classification of the order, taking into account all the known genera, but with particular reference to those from the Lower Ludlow of Saaremaa. *Witaaspis patteni* is synonymized with *W. schrenkii* and *Rotsiküllaspis obrutchevi* with *Saaremaaspis mickwitzi, Cephalaspis oeselensis* is referred to a new genus, *"Procephalaspis"*, and *Cephalaspis woodwardi* to another new genus, *"Stensiopelta"*. The classification of Dension is as follows:

"Order Osteostraci	
Family Trematapidae	
Subfamily Trematapinae	*(Trematapis)*
,, Dartmuthiinae	*(Dartmuthia, Saaremaaspis)*
,, Oeselaspinae	*(Oeselaspis)*
,, Didymaspinae	*(Didymaspis)*
Family Sclerodontidae	*(Sclerodus)*
,, Ateleaspidae	*(Hemicyclaspis, Hemiteleaspis, Micraspis, Aceraspis, Ateleaspis, Witaaspis)*
Family Cephalaspidae	
Subfamily Cephalaspinae	*(Thyestes, Procephalaspis, Cephalaspis)*
,, Benneviaspinae	*(Securiaspis, Benneviaspis, Hoelaspis, ? Boreaspis, Stensiopelta)*
Family Kiaeraspidae	*(Kiaeraspis)*."

General views as to the position of the group Osteostraci in the vertebrate system are expressed by Goodrich, de Beer and Watson (Goodrich 1931, de Beer 1931), and Sewertzoff (1931). Goodrich and de Beer i. a. lay stress upon the many points of agreement in the structure of the two recent cyclostomous groups and object to the supposition (advanced by Stensiö 1927) of a polyphyletic origin for them (similar views are expressed by Sewertzoff 1931). This opinion is also held by White (1935a), who places the Osteostraci as a class and order of its own among the Agnatha, in rank with the Heterostraci (exclusive of the Coelolepids), Anaspida and Cyclostomata, and by Watson (1937), who applies the same divisions.

The classification of Berg (1937; 1940) is somewhat different and is in agreement with that of Stensiö (1927) in so far as he separates the two recent cyclostomous groups; he divides the Agnatha into four classes: Cephalaspides (Osteostraci), Petromyzones, Pteraspides (Heterostraci) and Myxini. The Cephalaspides are made to contain the subclass Cephalaspides (with the orders Cephalaspidiformes and Trematapidiformes) and the subclass ? Birkeniae (Anaspida).

A similar conception of the larger groups within the Agnatha is found in a paper by Gross (1939), partly expressed in an earlier paper (Gross 1933c).

Moy-Thomas (1939) classifies the Agnatha in the following way:

"Sub-class 1. Ostracodermi
  Ord. 1. Heterostraci = Pteraspida
  Ord. 2. Coelolepida
  Ord. 3. Osteostraci = Cephalaspida
  Ord. 4. Anaspida
Sub-class 2. Cyclostomi."

Only the orders Osteostraci and Anaspida are thought to be closely related to one another; the Coelolepids are hesitatingly placed in the Agnatha; the possibility that the modern Cyclostomes may be the descendents from a cephalaspid- or anaspid-like ancestor is appreciatively discussed.

Heintz has also dealt with these questions; he adopts (Kiær & Heintz 1935) in some measure the classification of Stensiö (1927), but leaves open the question as to the relations of the recent Cyclostomes to the fossil groups. The divisions of Zych (1937) are in accordance with those of Stensiö.

Westoll (1945) discusses i. a. the possibility that some Coelolepids may be related to the Osteostraci (even the possibility that they may be "larval" Osteostraci), others to the Heterostraci, and yet others to the Anaspida. The evolution of the group Agnatha is considered by Obruchev (1945) in conjunction with a discussion of the development of the exoskeleton. Contrary to the views of Stensiö he assumes a progressive evolution from forms with small exoskeletal units towards forms with large and compound plates (cf. also "the lepidomorial theory" of Stensiö & Ørvig, see Ørvig 1951, pp. 366—368). The Thelodonti are regarded as the basal agnathous group from which the Heterostraci, the Osteostraci, the Anaspida and the recent Cyclostomata have evolved.

The systematic position of the group Heterostraci, as of interest in this connection, has lately been examined also by Balabai (1948).

Morphological questions connected with the Cephalaspids are dealt with by Allis (1931a, mouth-opening and visceral skeleton; 1931b, naso-hypophyseal canal), Bohlin (1941; sensory fields) and Holmgren (1942; sensory line system), and furthermore discussed in a greater or lesser degree in connection with investigations into the anatomy or embryology of *Petromyzon* by Damas (1943), Johnels (1948; 1950). and Lindström (1949).

Material and methods.

The cephalaspid material from Spitsbergen, treated in this paper, is on the whole of the same type as that described by Stensiö (1927); the fossils thus consist almost exclusively of cephalic shields or fragments of such shields. On one occasion only parts of the trunk have been found associated with the cephalic shield (a specimen of *Cephalaspis pinnifera)*. Parts or fragments of the detached trunk are present in two cases.

The types of the vertebrate-bearing rocks from the Spitsbergen Old Red, as far as of interest in this connection, have been described by Stensiö (1927, p. 18), Heintz (1929a, p. 21) and Kiær & Heintz (1935, pp. 17—18), and I can therefore in the main refer to these authors.

The rocks are different kinds of sandstone, which always are calciferous; in some places the rock has the character of a lime-sandstone. Often, especially in Mt Ben Nevis, the rock is conglomeratic, the conglomerate is intra-formational, and the small nodules consist of mud-stone fragments (cf. Heintz 1929a, p. 21). Concretion-like nodules, containing fossils, occur in a few places: Fraenkel Ridge, in the "Psammosteus" layer, Mt Ben Nevis, in the Vogti layer and on Mt Pteraspis (cf. Kiær & Heintz 1935, p. 17).[1]

As to the state of preservation of the fossils in different kinds of

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[1] The result of analyses of the lime-content of some sandstone types from Spitsbergen is shown below (the calcite was dissolved with acetic acid (4-n), in sample 4c with 5% and 4d with 10% hydrochloric acid; the weight of each sample was 20 g):

1.	Red Bay series.	Fraenkel Ridge, Primaeva layer	45.95%	$CaCO_3$
2.	,,	,, Anglaspis layer	28.15%	,,
3.	,,	Mt Ben Nevis, Benneviaspis layer	33.4 %	,,
4a.	,,	Andrée Glacier, S. half, moraine	64.5 %	,,
4b.	,,	,, ,, ,,	64.9 %	,,
4c.	,,	,, ,, ,,	68.45%	,,
4d.	,,	,, ,, ,,	45.5 %	,,
5.	,,	Mt Pteraspis	39.55%	,,
6.	Wood Bay series.	Mt Sigurd, slope towards the Hoffnung Gl. a) "red layers about 130 m"	40.0 %	,,
7.	,,	b) layer with *Boreaspis ceratops*	42.65%	,,
8.	,,	Mt Kronprinz, opposite the Stjørdalen Valley, grey sandstone	36.5 %	,,
9.	,,	Mt Lyktan, S. E. slope	27.0 %	,,

(Cont. overleaf)

rocks, we can, in addition to what has been said by Stensiö (1927) and Kiær & Heintz (1935), state that in some places in the Anglaspis layer on the Fraenkel Ridge the cephalic shields (preserved in a dark grey sandstone) are exceptionally well preserved, the inner parts, including the endoskeletal cavities and canals being filled with calcite, which makes the preparation comparatively easy. The shields from the Primaeva layer (in a reddish sandstone) are rather well preserved but the bone-tissue seems in many cases to have been subjected to some chemical alterations so that they will not readily or not at all stain with alizarin; the same applies to some shields from the lowermost part of the Wood Bay series on Mt Sigurd. Those shields occurring in a grey sandstone in the Wood Bay series are generally much better preserved than those embedded in the usual red or red-brown sandstone. The fossils from the light grey, coarse sandstone in Mt Borgen (Wood Bay series), being well preserved with regard to their external shape, have, however, the inner structures destroyed to a varying degree.

In general it can be said that the exoskeleton is badly preserved and does not show any finer details. The endoskeleton is often well preserved, and more often so in the specimens from the Red Bay series than in those from the Wood Bay series. The inner parts of the shields from the Wood Bay series are usually not well or not at all preserved, and this is very probably primarily due to unsuitable conditions during and after fossilization in the sandstones from this series, and possibly the bad state of preservation is to a certain degree caused by a feebler development of the endoskeletal bone-layers (cf., however, Stensiö 1927, pp. 31—32; 1932, pp. 12—13). The state of preservation varies in some species according to the type of rock in which the different specimens are embedded. We find e. g. that a specimen of *Cephalaspis laticornis* from a grey-green sandstone has at least the perichondrial canal-layers very well developed while the endoskeleton on the whole in other specimens of the same species, but occurring in the usual red sandstone of the same series, is badly preserved. In most of the specimens of *Nectaspis areolata* the endoskeletal bone-layers are more or less delicate or even absent but in two specimens from one locality on Mt Lyktan they are well and strongly developed (this applies also to two specimens of *Boreaspis robusta* from the same locality).

10a.	Wood Bay series.	Mt Lyktan, S. E. Slope, sandstone with *Nectaspis areolata* and *Boreaspis robusta,* holotypes	37.6 %	CaCO$_3$
10b.	„	ditto	38.05%	„
11.	„	Mt Lyktan, Fiskedalen Valley	33.12%	„
12.	„	Mt Borgen, N. part	13.15%	„
13.	„	Mt Errol White, “fossiliferous layer ab. 125 m”	34.3 %	„
14.	„	Stjørdalen Valley, S. side	20.6 %	„
15.	„	„ „ „ , W. part	23.7 %	„
16.	„	Mt Prismefjell, W. slope, about 200 m	21.2 %	„

Often the shape of the fossil shields has been affected by pressure of the rocks and they are thus more or less distorted. This is most often the case with shields from the Stjørdalen division of the Wood Bay series (see e. g. *Nectaspis dellei,* p. 547).

The fossils detach themselves from the embedding rock in such a way that the splitting plane lies either within the exoskeleton through the lower division of the middle layer or just beneath the exoskeleton in the zone of the subcutaneous canal plexus; an outer or peripheral part of the fossil thus almost invariably remains on the counterpart.

The preparation of the fossils was first carried out with the help of chisels, and then, under a low-powered binocular magnifier, with a dental mallet. The finer preparation was carried out by fine needles under a binocular microscope of the Greenough type, usually with a magnification of 25—40 times. During this finer preparation the fossils most often were soaked with alcohol, xylol, oil of aniseed, or coated with glycerine, and in such cases a strong illumination was used (as a Leitz "Monla"-lamp or a Reichert pointolit lamp). In some cases it was found very useful and practical to cut parts of the fossils, in which the deep lying canals or cavities were to be followed, in smaller or larger pieces by means of a pair of sharp pincers. The fossils could thus most often be cut as desired and the required canals exposed; if necessary the canals or cavities in these pieces were cleaned out with the dental mallet or with needles. After studying them in this way the fossils were "mended" by gluing together the pieces carefully. For photographing the fossils were often immersed in one of the fluids mentioned (or in a few cases in thick canada balsam) and lighted up with the aid of, usually two, strong arc-lamps. In a few cases the fossils were coated with ammonium chloride, and a soft illumination was used (cf. pls. 27:2; 39:3). Extremely useful in many cases was the staining of the bone-tissue with alizarin (using a saturated solution of alizarin in alcohol); the method has been fully described by Stensiö (1944, pp. 5—6); in the explanations to the plates in this paper it is always remarked when this method has been used on the fossils figured.

The measurements given in the systematic descriptions were always taken directly upon the fossils as they are preserved, thus e. g. small irregularities in the symmetry of the cephalic shields are not disregarded, even if they have possibly originated during the fossilization. Distinctly distorted shields are generally not directly measured but the very approximate dimensions of the restored shields are given. As in most cases it is impossible to say if the fossils have undergone some slight postmortal distortions or not, it is of course evident, that the figures referring to measurements must be used very cautiously, and cannot, in general, be used for more elaborate statistical calculations.

The thin sections through the exoskeleton for study of its minute structure were made in the ordinary way; it was, however, in many instances found useful first to embed the samples in a transparent plastic (methyl-metacrylate), in the main following the procedure described by Randall & Menzies (1941).

The grinding method for obtaining serial sections has not been employed.

All the photographs used for the plates or text-figures in this paper have been retouched.

List of localities.

(See the maps, figs. 1—3; the numbers on the maps refer to localities or groups of localities, to be found with corresponding figures in the following list. The maps are compiled from those in the papers of De Geer (1912; 1913), Isachsen (1915), Heintz (1929b), Lid (1929), Føyn & Heintz (1943). Many informations have been obtained from "The Place-Names of Svalbard" (1942). The statements as to longitude and latitude are not at all uniform for the different localities, and are in most cases only approximate.)

Localities at the bays of the North Coast (1—20).

Localities on the E. side of Red Bay (Raudfjord; 1—3).

1. Fraenkel Ridge (Fraenkelryggen), a narrow ridge from the S. part of Mt Fraenkel towards Red Bay, immediately N. of the Andrée Glacier (79° 41′ N., 12° 20′—30′ E.).

   On the labels the stratigraphical horizon only is indicated, and this refers in many cases to a certain locality or to localities within a rather restricted area; they can more or less exactly be placed with the aid of the statements by Heintz (in Kiær & Heintz 1935, pp. 11—13); as to the localities a) — c), see also Høeg 1942, p. 13.

   a) "Psammosteus lag" (horizon), on the easternmost part of the ridge, about 500—550 m. *(Cephalaspis corystis, C.* sp. no. A 30099);
   b) "Corvaspis lag", "Corvaspis horizon", on the N. side of the ridge, along a brook from the glacier on the W. slope of Mt Fraenkel *(C. acuminata, C. dissimulata);*
   c) "Plante lag" (Plant horizon), as b) but further down *(C. cradleyensis, C. pygmaea);*
   d) "Primaeva lag", "Primaeva horizon", different localities in a red sandstone in the middle parts of the ridge, S. of b) *(C. acuminata, C. dissimulata, C. divaricata, C. eurhynchus, C. heintzi, C. hyperboreus, C. oreas, C. pygmaea, C. sinuata, C. verruculosa, Ectinaspis heintzi);*

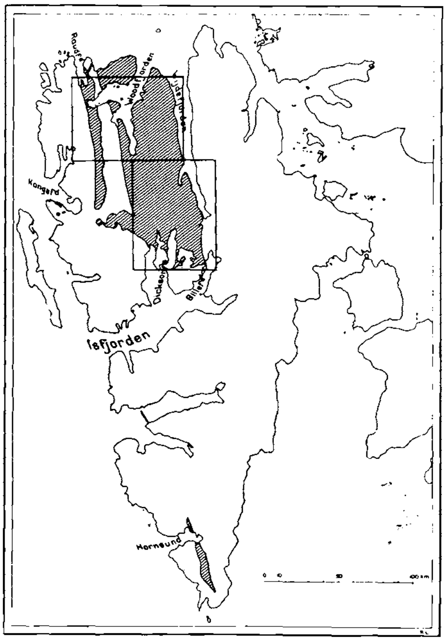

Fig. 1. — Map of Spitsbergen, showing the extent of the Devonian system (after Høeg 1942). The framed square fields denote the areas, shown on a larger scale in figs. 2 and 3.

e) "Polaris lag" (horizon), "Horis. 250 m.", in a grey-green sandstone in the middle parts of the ridge; its relation to d) seems to be obscure *(C. arcticus, C. dissimulata, C. oreas?);*

f) "Anglaspis lag", "Anglaspis horizon", "Horis. 200 m.", on the S. W. side of the ridge, on the slope towards the Andrée Glacier *(C. acuminata?, C. deltoides, C. dissimulata, C. divaricata?, C. eurhynchus?, C. excellens, C. hastata, C. recticornis, C. vogti, C.* sp. ENS nos. 608, 610).

2. Between Fraenkel Ridge and Mt Ben Nevis;

a) Andrée Glacier (Andréebreen); in the moraine (without further annotation of locality) *(C. tenuicornis, Securiaspis* sp.);

b) Andrée Glacier, N. half, W. part; in the moraine (moraine material originating from Fraenkel Ridge) *(C. eurynotus?, C. verruculosa?);*

c) Andrée Glacier, S. half, W. part; in the moraine (moraine material derived from Mt Ben Nevis) *(C. broughi, C. ibex, C. metopias, C. pinnifera, C. platycephalus, C. tenuicornis, C.* sp. ENS no. 611, *Tegaspis kolleri);*

d) W. of the Andrée Glacier *(C. eurynotus, C. powriei* var. *polaris, C. sinuata, C. verruculosa?);*

e) in the shore profile ("Strand profil"), very probably on the N. side of the stream from the S. W. corner of the Andrée Glacier *(C. eurynotus).*

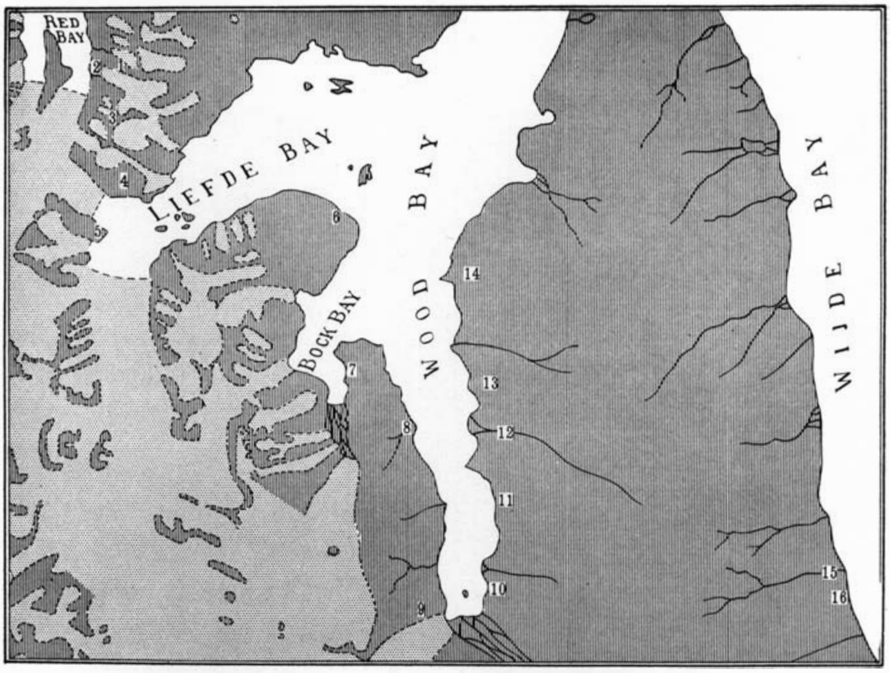

Fig. 2. — Sketch-map of a northern part of W. Spitsbergen, with fossil localities 1—19. Scale 1:625 000.

Unglaciated areas in the western part are strongly shaded; in the eastern part the whole land-area is strongly shaded; on the whole this area is much less glaciated than the western part.

The area mapped adjoins the area shown in fig. 2; cf. fig. 1.

3. Mt Ben Nevis. Mountain E. and S. E. of the head of Red Bay, S. of the Andrée Glacier (79° 39′ N., 12° 26′ E.);
   - a) without annotation of the exact locality, in talus *(C. aarhusi, C. crofti, C. eukeraspidoides, C. exilis, C. hoeli, C. pinnifera, C. platycephalus, C. retusa, C. tenuicornis?, Benneviaspis holtedahli, S. quadrata, S. staxrudi, T. kolleri);*
   - b on the shore [of Red Bay] *(C. signata);*
   - c) N. W. part, "S. of the Andrée Glacier, fossiliferous horizon about 50 m above sea level" *(Benn. holtedahli?);*
   - d) Northern Plateau, 300 m *(C? pedata),* 600 m *(Benn. longicornis);*
   - e) "Vogti lag" (horizon), on the Northern Plateau or Northern Ridge *(C. føyni, C. ibex);*
   - f) horizons A-I (of Hoel), on the N. side of the brook from the First Glacier on Mt Ben Nevis to the Grand Glacier S. of Red Bay *(S. staxrudi, T. kolleri);*
   - g) Second Glacier (on the W. slope of the mountain), in the moraine ("Cephalaspis moraine") *(C. metopias, C. signata, C. tenuicornis, T. kolleri);*

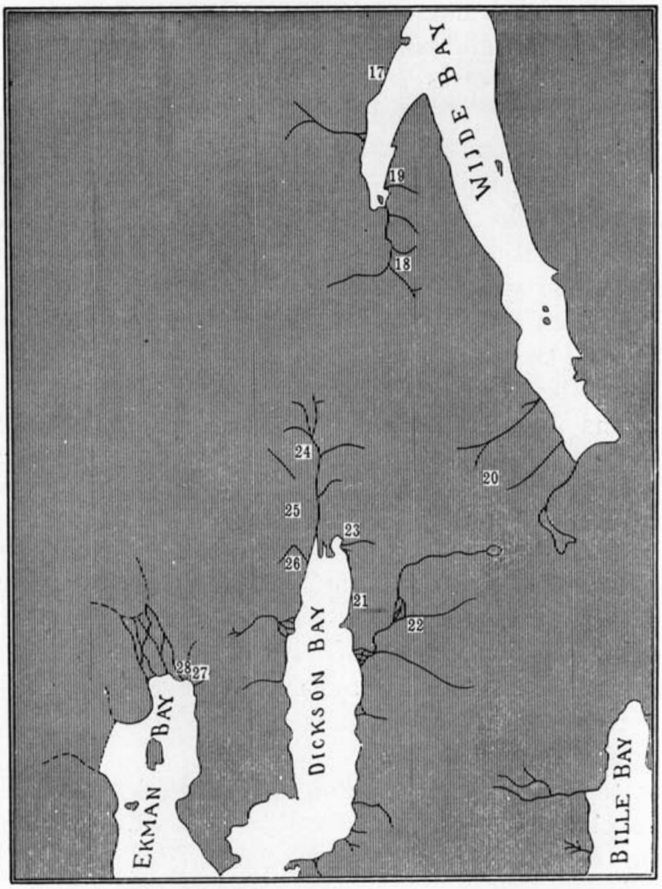

Fig. 3. — Sketch-map of a central part of W. Spitsbergen, with fossil localities 20—28. Scale 1:625 000.

The whole land-area is shaded (no distinction is made between glaciated and unglaciated areas). The map is to the N. continued by that in fig. 2; cf. fig. 1.

h) "Tunge", a narrow tongue between the upper parts of the First and Second Glaciers *(Benn.* sp. 1, *C. hastata?, C. hoeli, C. signata);*

i) the Cliff, immediately S. of f), forming the N. escarpement of j) (= "below Southern Plateau") *(C. crofti, C. ibex);*

j) Western Plateau, S. of the First Glacier, W. of the top of the mountain,

300—400 m, "Ctenaspis lag" (horizon) *(Benn. holtedahli, B. platessa?, C. doryphorus, C. exilis, C. hoeli, C. platycephalus, C. retusa),*

500—600 m, "Benneviaspis lag" (horizon) *(Benn. holtedahli, B. platessa, C. exilis, C. hoeli, C. metopias, C. retusa,* *Hoelaspis angulata, Kiaeraspis auchenaspidoides, S. staxrudi, T. kolleri);*

k) S. W. part *(Kiaeraspis auchenaspidoides);*

l) horizons J-U (of Hoel), localities on the S. W. slope of the mountain, from the glacier between Wulff Ridge and Mt Ben Nevis to the top of the mountain *(C. retusa);*

m) S. E. slope, in talus *(T. kolleri).*

The place of some localities has been determined after the statements in the paper by Kiær & Heintz (1935, pp. 11—15). It has not been possible to indicate these localities from Mt Ben Nevis (and those from Fraenkel Ridge) on the map, fig. 2, but they may be placed with the aid of the detailed map and the panorama in Kiær & Heintz (1935, pp. 11—13), to which the reader is referred.

Localities at Liefde Bay (Liefdefjorden; 4—6).

4. Mt Pteraspis (Pteraspistoppen), mountain on the W. side of the bay, near its head, between the Ida Glacier in the S. and the Erich Glacier in the N. (79° 36′ N., 12° 30′ E.) *(C. deltoides, C. recticornis, C. sinuata.)*
5. "The mountain S. of the Ida Glacier" (between the Ida and Emma Glaciers; E. part of Mt Ringertz); N. side (79° 34′ N., 12° 26′ E.) *(C. exilis).*
6. Cape Roos (Roosneset; point on the peninsula between Liefde Bay and Bock Bay); N. slope of the Roos Mts (Roosfjella; incorrectly as the K. Wilhelm Mtn on the label; 79° 35′ N., 13° 28′ E.) *(Boreaspis gracilis).*

Locality on the E. Side of Bock Bay (Bockfjorden; 7).

7. Mt Kronprinz (Kronprinzhøgda), W. slope (79° 27′ N., 13° 30′ E.) *(Axinaspis whitei, Bor. circinus, B. puella?, B. intermedia, B. macrorhynchus?, B. robusta, C. caroli?, C. laticornis, C. oblonga, Nectaspis peltata?).*

Localities at Wood Bay (Woodfjorden, Vedafjorden; 8—14). Localities on the W. side of the bay (8—9).

8. Mt Kronprinz (Kronprinzhøgda , mountain forming the peninsula between Bock Bay and Wood Bay; S. E. part, on the E. Slope of the mountain, "opposite the V. Stjørdalen" (79° 25′ N., 13° 46′ E.) *(Acrotomaspis instabilis, Bor. circinus, B. gracilis, B. macrorhynchus, B. robusta, B. spinicornis, B. triangularis, B.* sp., *C. fracticornis, C.* sp. ENS no. 606, *N. peltata).*
9. Mt Sigurd (Sigurdfjellet), mountain near the head of the bay (79° 14′—18′ N., 13° 23′—54′ E.). The localities are situated in the N. E. part of the mountain;

a) on the slope towards the Hoffnung Glacier (Vonbreen), about 6 km from the coast, in a grey-green sandstone *(H. angulata);*

b) as a) but nearer to the coast, in red sandstones (most of the fossils are found in talus, some in "red layers, about 130 m", an information of little value, since the layers do not lie horizontally) *(Ax. whitei, Benn. grandis, B. lövgreeni, B. maxima, Bor. batoides, B. ceratops, B. costata?, B. intermedia, B. macrorhynchus, B. puella, B. rostrata, C. curta, C. fracticornis, C. isachseni(?), C. jarviki, C. laticornis, C. oblonga?, C. producta);*

c) "E. slope, 0—500 m" (slope towards Wood Bay) *(C. brevicornis?, C. oblonga?).*

The indication "Wood Bay. I Bunden" (Wood Bay, at the head of the bay) on old labels refers to locality (localities) on the slope of Mt Sigurd towards the Hoffnung Glacier.

Localities on the E. side of the bay (10—14).

10. Mt Wächter (Vaktaren), mountain E. of the head of Wood Bay (79° 16′ N., 13° 13′ E.); on the slope towards the bay *(C. gigas, C. oblonga?).*
11. Mt Scott Keltie (Scott Keltiefjellet), mountain-complex N. of Mt Wächter (79° 19′—25′ N., 14° 2′—30′ E.);
    a) S. side, slope towards the valley between this mountain and Mt Wächter *(Bor. costata, B. robusta);*
    b) S. part, W. slope *(Bor. gracilis, B. robusta, C. gigas?, C.* sp. ENS no. 607);
    c) N. part, W. slope, at 500 m *(Acr. trinodis),* in talus *(C. producta?).*
12. Stjørdalen Valley, valley between Mt Scott Keltie and Mt Sørli (the mouth at about 79° 25′ N.); slope of the northernmost part of Mt Scott Keltie;
    a) S. side *(C. curta?, C. semicircularis, N. areolata, N. dellei);*
    b) S. side, W. part *(C. moy-thomasi, C. semicircularis).*
13. Mt Sørli (Sørlifjellet), mountain between Stjørdalen Valley and Verdalen Valley (79° 25′—29′ N.);
    a) without indication of exact locality *(Bor. robusta, C. moy-thomasi);*
    b) "between V. Stjørdalen and V. Vaerdalen, 0—500 m, talus" *(Acr. trinodis, Bor. robusta, N. dellei).*
14. Mt Prismefjellet, mountain N. of Verdalen Valley, at Cape Auguste Viktoria (79° 31′ N., 14° E.); W. slope, 200 m *(Acr. trinodis?).*

Localities on the W. side of Wijde Bay (Wijdefjorden, Videfjorden; 15—20).

15. Sixth Valley (Sjettedalen), about 79° 21′ N. *(C.* sp. ENS no. 609).

16. S. of the 6th Valley, in the coast-profile *(Acr.* sp. 2).
17. Mt Errol White, mountain at the entrance of Vestfjorden, the W. branch of Wijde Bay ("the mountain S. of Sneugledal" = Krosspynt Valley), between Krosspynt Valley and Landing Valley (79° 13′ N.);
    a) without note of exact locality *(Bor. curtirostris, C.* sp. no. A 30098, *N. areolata);*
    b) E. slope, fossiliferous horizon about 125 m above sea level *(Bor. robusta, N. areolata (?)).*
18. Between Bryhn Valley and Kaalaas Valley, on the E. side of Vestfjord Valley (between these valleys lies the Hagen Valley, and the exact locality is, without doubt, S. of this valley, about 79° 6′ N.) *(C. caroli).*
19. N. of Jørgensen Valley, on the E. side of Vestfjorden (about 79° 8′ N.) *(Bor. robusta).*
20. Passage between Jäderin Valley and Zeipel Valley, on the W. side of the innermost part of the East Fiord (Austfjorden, the E. branch of Wijde Bay; 78° 54′ N., 16° E.), 590 m *(Benn.* sp. 2).

Localities at the northern bays of the Ice Fiord (Isfjorden; 21—28).
Localities at Dickson Bay (Dicksonfjorden; 21—26).

21. Mt Lyktan (Lykta), mountain at the E. side of the inner part of the bay, bounded in the S. and E. by Nathorst Valley, in the N. by Fiskedalen Valley; the N. part of the mountain is called Mt Fiskefjellet (78° 48′ N., 15° 30′ E.);
    a) S. E. slope *(Bor. gracilis, B. robusta, C. lanternaria, N. areolata);*
    b) S. W. slope *(Bor. robusta, B. spinicornis, C. lanternaria?);*
    c) W. slope *(Bor. curtirostris, N. areolata);*
    d) the shore profile *(Bor. costata);*
    e) Fiskedalen Valley (Soppdalen) *(Bor. curtirostris, B. robusta, N. areolata).*
22. Mt Triplex (Triungen), mountain S. E. of Mt Lyktan, between Culm Valley in the N., Nathorst Valley in the N. W. and Hugin Valley in the S. and S. W. (78° 45′ N., 15° 42′ E.); N. slope, towards Culm Valley *(Bor. curtirostris, B. gracilis?, B. robusta, N. areolata).*
23. Mt Rebbingen ("the Mt. N. of Fiskedalen"), mountain on the E. side of Dickson Valley, N. of Mt Lyktan, between Fiskedalen Valley (Soppdalen) in the S. and Grønhorg Valley in the N. (78° 51′ N., 15° 30′ E.); S. W. slope *(Bor. costata, B. robusta, C. gigas?, N. areolata).*
24. Mt Barmfjellet, mountain on the W. side of Dickson Valley, between the Battye Glacier (Trevor-Battye Glacier) in the N. and Flat Valley in the S. (78° 54′ N., 15° 12′ E.) *(Bor. gracilis, B. robusta, C. gigas, C. laticornis).*

25. Perched Block Mtn, on the W. side of Dickson Valley, between Mt Borgen and Mt Barmfjellet *(C. gigas?, N. areolata).*
26. Mt Borgen, mountain on the W. side of the innermost part of Dickson Bay, opposite Mt Lyktan (78° 48′ N., 15° 12′ E.); N. part *(Acr.* sp. 1, *Bor. costata, B. curtirostris, B. robusta, C. menoides, N. areolata).*

Localities on the E. side of Ekman Bay (Ekmanfjorden; 27—28).

27. The mountain N. of Mt Garborg (Garborgnuten; 78° 44′ N., 14° 52′ E.); W. slope *(N. areolata).*
28. The second mountain N. of Mt Garborg (78° 45′ N., 14° 48′ E.);
    a) S. part *(N. areolata);*
    b) N. W. part *(N. areolata).*

General anatomical remarks.[1]

External features of the cephalic shield.

The following general anatomical description must only be taken as remarks upon the anatomy of the Spitsbergen Cephalaspids. For a comprehensive account of the general anatomy the reader is referred to the basic paper by Stensiö (1927). It has been found that the structure of the Cephalaspids is rather uniform (cf. Stensiö 1932, p. 28), and that the different forms in the new material, here treated, as to their inner structure, in general fit in with the descriptions of Stensiö, which mainly are based upon very penetrating investigations of two (three) species, *Cephalaspis hoeli* (incl. *C. exilis)* and *Kiaeraspis auchenaspidoides.*

The remarks given in this section of the paper refer therefore in general to conditions, different from those found by Stensiö, or to features, better preserved here than in his material, or to interpretations, in which I differ from those expressed by earlier investigators.

The cephalic shield of the Osteostraci (= Cephalaspida) is, as demonstrated by Stensiö (1927), composed of different parts, viz. a cephalic division or the cephalic shield proper, and an abdominal division, comprising the unpaired inter-zonal part of the shield and the paired zonal parts (or the shoulder-girdle). These parts are rigidly and without apparent boundaries united with each other so as to form the continuous cephalic shield.

The shape of the cephalic shield in the Spitsbergen Cephalaspids is in general fairly uniform, the shield being more or less triangular in outline with its postero-lateral parts produced into cornua of varying length.

The genera *Kiaeraspis, Axinaspis, Acrotomaspis* and *Nectaspis* form exceptions to this rule. In these genera the cephalic shield (figs. 100—106; pls. 97—98; 100—106; 108; 110—113) is oblong, owing partly to a feeble development *(Kiaeraspis)* or even absence *(Axinaspis, Acrotomaspis, Nectaspis)* of the cornua, and partly to a lengthening of the shield. This lengthening of the shield affects the inter-zonal part

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[1] The terminology used in this paper follows (when not otherwise stated) that employed by Stensiö (1927; 1932), and for its explanation the reader is referred to these papers.

in *Kiaeraspis* (Stensiö 1927, pp. 24, 297; 1932, p. 8; cf. p. 37) and to a lesser degree also in *Axinaspis* and *Acrotomaspis,* but is in *Nectaspis* mainly due to a strong development of the pre-orbital part of the shield.

In some forms the shield is provided with processes of different kinds, viz. besides the lateral cornua, commonly present, also a rostral process or a dorsal spine. These processes are thus integral parts of the cephalic shield, and when in the descriptions in the systematic part the term cephalic shield is used, they are (when present) included. The term main cephalic shield (this is only a descriptive term without any morphological meaning, and should not be confused with the cephalic shield proper) denotes the central part of the cephalic shield exclusive of these processes.

The cephalic shield is broadest at a level across the cornua or the basis of them and is more or less rapidly decreasing in breadth anteriorly.

The rostral margin of the shield in most species is evenly rounded or obtusely angular but in some species of *Cephalaspis* the shield is produced into a short rostrum, fairly indistinct (pls. 3; 5:1-2; 7) or rather evident (pls. 4; 5:4-6), but always gradually merging into the main cephalic shield. In the genera *Hoelaspis* and *Boreaspis* there is a short or long rostral process, distinctly set off from the rest of the shield (figs. 85—99; pls. 76; 78—80; 82—92; 94—95; cf. Stensiö 1927, pls. 13—15).

In *Nectaspis,* as noted above, the pre-orbital part of the shield including the roof of the buccal cavity is somewhat prolonged, but the rostral part of the shield is not produced into any rostrum or rostral process.

In *Acrotomaspis* the rostral margin is truncate (pls. 101; 102:2; 104:3-4; 105); when the shield of *A. instabilis* is viewed obliquely from in front (pl. 102:2), it is seen that the antero-lateral borders of the shield are vertical and fairly high but that the rostral margin forms a much lower, antero-ventrally directed narrow rim; the shield can thus be said to be provided anteriorly with a low and broad ventral notch. These conditions can be explained by the assumption that an anterior (rostral) part of the ventral rim is not developed in this form, very probably owing to the fact that the mouth-opening has shifted from a subterminal (which is the normal one in the Cephalaspids) to a more terminal position. In geologically younger species of the same genus the rostral margin is indistinctly indented (*A.* sp. 1, pl. 104:3) or distinctly trilobated *(A. trinodis,* pl. 105; *A.* sp. 2, pl. 104:4), the antero-lateral corners of the shield and a median part of the rostral margin being somewhat produced anteriorly.

The sensory fields ("electric fields" of Stensiö; cf. p. 192) consist invariably of one unpaired dorsal field besides one or several pairs of lateral fields. Normally there is only one pair of lateral fields as in

Cephalaspis, Securiaspis, Tegaspis, Ectinaspis, Benneviaspis, Hoelaspis, some *Boreaspis* species, and generally in *Kiaeraspis.*

In *Boreaspis ceratops* (fig. 98; pl. 96) the margins of the lateral fields are incised in their middle parts in such a way that each lateral field is partly subdivided into an anterior and a posterior portion. In one specimen of *B. curtirostris* (fig. 96C; pl. 92:3) and one specimen of *Kiaeraspis auchenaspidoides* (fig. 100B; pl. 97:2) the lateral field is actually divided into two divisions (lsf_1, lsf_2) by a very narrow space. In the following *Boreaspis* species, viz. *B. circinus* (fig. 95; pls. 90:1; 92:2), *B. spinicornis* (fig. 93; pl. 89:2-4) and *B. triangularis* (fig. 94; pl. 90:4) the lateral fields are constantly subdivided into two parts, and we thus have here two pairs of lateral sensory fields (lsf_1, lsf_2).

In *Axinaspis* also there are two pairs of lateral fields (fig. 101A, B, D; pl. 97:4, lsf_1, lsf_2) or, expressed in another way, each lateral field is represented by two well separated divisions, corresponding to those in the specimen of *Kiaeraspis auchenaspidoides,* mentioned above.

In *Nectaspis* the lateral fields are each subdivided into three divisions (figs. 104—106; pls. 108; 111:2; 113:1, lsf_1—lsf_3), which in *N. peltata* (fig. 104; pl. 113:1) and some specimens of *N. areolata* (p. 545) are separated from each other by very narrow gaps.

In *Acrotomaspis* finally there are four lateral sensory fields on each side of the shield (figs. 102—103; pls. 101:1; 102:1-2; 103:1-3; 104:4; 105:4; lsf_1—lsf_4).

As is evident from the survey of the lateral sensory fields in different Spitsbergen Cephalaspids, I regard the presence of more than one pair of lateral sensory fields as a secondary character, being the result of a subdivision of a primarily single pair of fields. The conditions in *Kiaeraspis, Axinaspis* and *Acrotomaspis* are assumed to represent different stages in an evolutional series. As is shown by the innervation of the lateral fields (see pp. 129, 205; cf. figs. 101B, 105C) the conditions in *Nectaspis* cannot, however, be regarded as a further development of the stage represented in *Axinaspis.* In this connection I may mention that the presence of two pairs of lateral sensory fields in *Tremataspis* also is interpreted as a secondary condition (see p. 556).

The shape of the dorsal and the lateral sensory fields is very varying (as is seen in the systematic part). Suffice to mention here that the lateral fields (or the posterior pair of lateral fields) in some *Benneviaspis* species (figs. 81—82; pls. 73; 75:1, *lsf*), in *Boreaspis* (e. g. figs. 86—99; pls. 78:3; 79:2; 90:1; 92:3), *Acrotomaspis* (figs. 102—103; pls. 101; 102:1; 103:3; 104:4; 105:4, lsf_4) and *Nectaspis* (figs. 104—106; pls. 108; 111:1-2; 112:3; 113:1, lsf_3) extend to or are (partly) situated on the dorso-lateral sides of the inter-zonal part of the shield, that they do not at all continue upon the cornua in *Tegaspis* (fig. 75; pls. 65:1; 66), *Boreaspis* (e. g. figs. 86—89; pls. 79:2; 80:2; 89:2-4; 91; 96) and *Kiaeraspis* (fig. 100A, B; pl. 97:1), and that both the dorsal and the lateral fields are very strongly developed in some species of *Benneviaspis* (figs. 81—82; pls. 73; 74; 75:1).

The exoskeletal plates of the sensory fields are found preserved only (on the lateral fields) in one specimen of *Cephalaspis pinnifera* (pls. 92:1; 93:2, *plsf)* and in some specimens of *Tegaspis kolleri* (pls. 65:1, *plsf;* 66; 116:1). In this latter species the plates seem to be more rigidly connected to the shield than is usual in the Cephalaspids, and a plate is in one place found to be anchylosed to the shield at the lateral margin of the field (pl. 116:1; see also p. 48).

The naso-hypophyseal opening normally consists of the ordinary three divisions, but in *Boreaspis* the anterior and middle divisions are represented by a more or less slit-like opening while the posterior division is oval or rounded (pls. 78:1; 79:2; 80; 88:1-2; 90:2-3; 91:2; 92:3-4; 95:2). In most of the *Benneviaspis* species the whole opening is slit-like and linear without any divisions (fig. 4C; pls. 70:2; 71:1; 72:2; 73; 74); in the species *B. longicornis* (pl. 68:3), however, the naso-hypophyseal opening has the normal form. In *Acrotomaspis instabilis* the opening is unusually large (pl. 101).

In *Nectaspis* the middle division of the opening is obliterated, the lateral borders of this divison being united with each other, leaving at most a suture between them (pls. 108; 110:2, na_1, na_2; 111:2, na_1, na_2; 112:3), and we have thus one anterior opening for the hypophyseal duct and one posterior nasal opening. The same conditions are to be found in a few *Cephalaspis* species, viz. constantly in *C. excellens* (fig. 4B, na_1, na_2; pls. 12:2, na_1, na_2; 13; 15:2), in *C. eurynotus* (pl. 18:2), and in two specimens of *C. dissimulata,* but in all these forms no trace of any suture is seen.

The anterior division of the naso-hypophyseal opening (or the separate opening for the hypophyseal duct) is usually situated most anteriorly and in the deepest part of the circum-nasal fossa, while the posterior division (or the nasal opening proper) is found on a small nasal elevation (as noted by Stensiö 1932, p. 4; see fig. 4A, B). In *Nectaspis,* however, also the opening for the hypophyseal duct lies on a separate small elevation in the anterior part of the circum-nasal fossa just in the same way as the nasal opening in its posterior part (pl. 110:2, na_1, na_2), and in *Benneviaspis* (distinctly seen in *B. maxima)* the whole slit-like naso-hypophyseal opening lies on a low nasal ridge (fig. 4C; pl. 74).

The circum-nasal fossa is often well developed, e. g. in many *Cephalaspis* species (fig. 4A—B, *fcn;* pls. 5:2; 7:1; 11:3-5; 12:2, 4; 13; 15:2; 23:1; 24; 26:1; 27; 29:1; 34:3; 36:1-2; 37; 38:2; 41), in *Securiaspis* (pl. 61), *Tegaspis* (pls. 65:1; 66), *Ectinaspis* (pl. 67:2), *Axinaspis* (pls.

97:4; 98:1), *Acrotomaspis* (pls. 101; 102:1,3), *Nectaspis* (pls. 110; 111), as well as in *Kiaeraspis* (Stensiö 1927, fig. 3). It is broad and fairly shallow in *C. gigas* (pl. 52) and *C. lanternaria* (pl. 54). In some *Cephalaspis* species an anterior division of the circum-nasal fossa is well defined and deep (e. g. pls. 26:1; 42:1, *fcn;* 43:2). The fossa is not well defined in *Benneviaspis* (fig. 4 C, *fcn;* pls. 68:3; 70:2; 73; 74) and in *Boreaspis* (pls. 78:1,3; 80; 88:1,2,6; 95).

On each side of the posterior part of the circum-nasal fossa, anteriorly or antero-medially to the orbits, there is in some species a more or less well defined or distinct elevation, for which the term antorbital prominence is adopted (after Lankester 1870a, p. 37). It is found in many *Cephalaspis* species (e. g. fig. 4A, B, *ap;* pls. 12:1, *ap;* 15:2; 18:2; 23:2; 24; 26:1; 27; 34:2, *ap;* 36:1; 41; 54), in *Securiaspis* (pl. 61), in *Tegaspis* (pl. 65:1), and in *Axinaspis* (pls. 97:4; 98:3); in *Benneviaspis* (see e. g. fig. 4 C; pl. 74) it is very faintly developed.

No pineal plate is found preserved in any Cephalaspid specimen from Spitsbergen but its existence is in many species indicated by the pineal depression, as e. g. in *C. excellens* (fig. 4 B, *pd;* pl. 15:2), *C. ibex* (pl. 36:1) and *C. hastata* (pl. 36:2). When the endoskeleton is not ossified, not preserved, or else not accessible for observation, the existence of a pineal plate in the living animal is indicated by a slit-like opening in the exoskeleton, extending transversely between the two orbital openings (cf. Heintz 1939, p. 17). This open space was once occupied by the pineal plate. The opening is here called the pineal fissure (fissura pinealis). It is distinctly seen in several *Cephalaspis* species (e. g. pls. 5:1; 6:1; 9:3; 12:2-3; 18:2; 23:1-2; 24). In *C. signata* (pl. 28:1) it is very narrow, and in *C. aarhusi* it is in its lateral parts extremely narrow and cannot possibly have lodged a pineal plate. There is, however, most anteriorly a small notch in the left lateral margin of the dorsal sensory field, indicating the possible presence in the living animal of a short transverse pineal plate along the anterior margin of the dorsal sensory field. In other *Cephalaspis* species the anterior and posterior borders of the pineal fissure have evidently approached each other so closely that they have met, and only a more or less distinct suture is left between the original borders; such a suture is distinctly seen in some species (fig. 4A; pls. 11:7; 19:2), more indistinctly in others (as in pl. 7:1). Thus in these species an independent pineal plate has never been present.

A pineal plate was present in the following *Cephalaspis* species, viz. *C. aarhusi* (possibly), *C. acuminata, C. eurhynchus, C. deltoides, C. divaricata, C. oreas, C. heintzi, C. pygmaea, C. dissimulata, C. eukeraspidoides, C. hyperboreus, C. excellens, C. vogti, C. eurynotus, C. verruculosa, C. sinuata, C. signata, C. ibex, C. doryphorus* (probably); its presence in *C. cradleyensis, C. føyni,* and *C. broughi* could not be

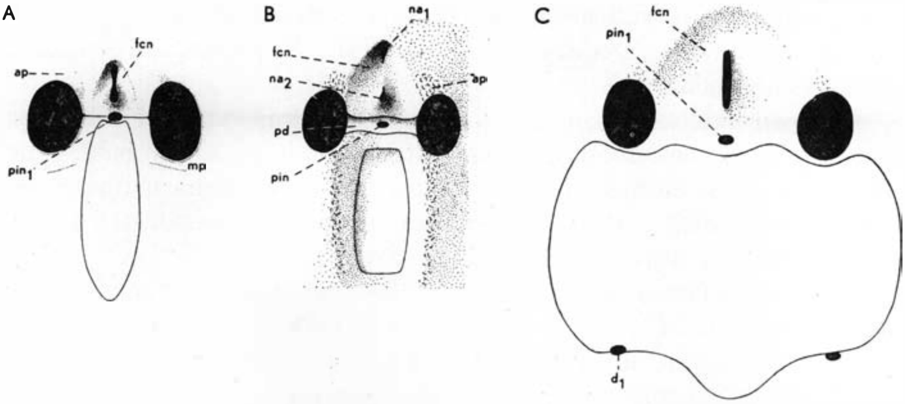

Fig. 4. — Dorso-median part of the cephalic shield, A, in *Cephalaspis hoeli,* B, in *Cephalaspis excellens,* C, in *Benneviaspis maxima.* A, B, × 2.5, C, nat. size.

ap, antorbital prominence; d_1, opening of the ductus endolymphaticus; *fcn,* circumnasal fossa; *mp,* anterior transverse sensory line; na_1, opening of the hypophyseal duct; na_2, nasal opening proper; *pd,* pineal depression; *pin,* pineal opening; pin_1, pineal opening on dorsal side of the exoskeleton.

ascertained. In *C. broughi* (pl. 7:1) the pineal opening on the dorsal side of the endoskeleton lies in the anterior end of the dorsal sensory field, and there possibly existed along the anterior margin of the field a short pineal plate (such as assumed in *C. aarhusi),* which did not reach laterally on to the orbital openings. In all the other Spitsbergen species of *Cephalaspis* an independent pineal plate was not developed and it can be noted that it is constantly absent in all the geologically young (the post-Dittonian) species of the genus, while in the Dittonian species the conditions were not stabilized.

The pineal plate is lacking in *Securiaspis* (see pls. 62:1; 63:2), *Tegaspis* (pl. 65:1), *Benneviaspis* (pls. 70:2; 71:1; 72:2; 73), *Hoelaspis* (pl. 76:1), *Boreaspis* (e. g. pl. 78:1, 3), *Kiaeraspis* (pl. 97:1, 2), probably in *Axinaspis* (there is in any case no long pineal plate, reaching from one orbit to the other; pl. 97:4), *Acrotomaspis* (pl. 101), and in *Nectaspis* (pl. 110:2). It was present in *Ectinaspis* (pl. 67:2).

In this connection it is worth while to denote the presence of a pineal plate in all the genera belonging to Ateleaspidinae (Stensiö 1932, pls. 1; 2:4; 3:4; 4:1-2; 5:2,3,5; 7:4; Heintz 1939, pls. 1; 3; 23:1; 30:3; pp. 25—26, 72, 89; Westoll 1945, pl. 61:1; p. 342), in *Tremataspis* (e. g. Patten 1912, figs. 238—239; Robertson 1938a, fig. 3; pl. 2:4; p. 187), in *Thyestes* (e. g. Stensiö 1932, fig. 13; pls. 27:4; 51:2; pineal depression), in *Witaaspis* (Schmidt 1894, figs. 3,8, pineal fissure; Robertson 1940a, p. 298; Denison 1951a, fig. 30B), *Dartmuthia* (Robertson 1935a, figs. 2—3, 5; p. 331; Denison 1951a, fig. 29 D), *Saaremaaspis* (Robertson 1938b, pp. 489, 491; pl. 60:6; Denison 1951a, fig. 29C). The plate is lacking in *Didymaspis* (Stensiö

1932, pl. 55:3-4), and probably also in *Oeselaspis* (Robertson 1935b, p. 458; cf., however, Denison 1951a, fig. 29B). Its presence in *Sclerodus* is not established.

As an independent pineal plate thus occurs in many of the oldest known forms, representing different families, it seems probable that this plate is an archaic feature, present in the ancestors to these different Osteostraci, and that its absence can be interpreted as a secondary condition, arisen independently in later forms.

In *Acrotomaspis trinodis* (pl. 105), no pineal foramen in the exoskeleton has been observed in the inter-orbital space, and it seems very probable that the distal end of the pineal organ was covered by an exoskeletal membrane as in the Heterostraci.

The openings of the ductus endolymphatici, which usually lie within the dorsal sensory field (e. g. pl. 78:3) or near its lateral margin (e. g. pls. 6:1; 8:1; 71:2, d_1; 77:2, d_1), are in *Cephalaspis jarviki* distinctly seen to open on the dorsal face of the exoskeleton behind the dorsal sensory field (pl. 46:2, *d*).

On the ventral side of the cephalic shield the oralo-branchial fenestra is seen in a few specimens; it is generally rounded in outline (figs. 100C; 101C; 102D; pl. 38:1), even in forms with very broad shields (pl. 50:1), and in *Benneviaspis* is somewhat broader than long (figs. 78E; 83B; pl. 75:2).

The postero-median zone of the ventral rim, which borders the fenestra oralo-branchialis posteriorly, is medially slightly produced, its margin towards the fenestra being somewhat convex, in *Benneviaspis* (figs. 78E; 83B; pl. 75:2). In *Axinaspis* and *Acrotomaspis* there is formed a distinct triangular (in *Acrotomaspis* bilobed) median process into the oralo-branchial fenestra (figs. 101C; 102D; pls. 99:1; 104:1-2). Also in *Kiaeraspis* (fig. 100C; cf. Stensiö 1927, pls. 52; 53:2; 58) there is a short median process, and this feature is also to be found in *Tremataspis* (see e. g. Patten 1903, fig. 8; Robertson 1938a, fig. 2; p. 197) and *Saaremaaspis* (Rohon 1892, pl. 1:18; Robertson 1938b, pl. 60:1-2, 4-5, 7; pp. 492, 489).

The cornua, which constitute the produced lateral parts of the zonal part of the shield or the shoulder-girdle, are most often well developed and project in a posterior or postero-lateral direction. They are laterally and somewhat posteriorly directed in *C. deltoides* (fig. 29; pl. 5:1-2), *Ectinaspis* (fig. 76; pl. 67), some *Boreaspis* species (figs. 89—91, 95, 97; pls. 86:1; 87; 88:1; 89:6; 90:1; 92:1-2; 93:1; 94; 95), laterally and only slightly posteriorly in *Benneviaspis longicornis* (fig. 77; pl. 68:3) and *Boreaspis ceratops* (fig. 98; pl. 96). In *Hoelaspis* they project in a lateral and slightly anterior direction with the very apex of the cornua pointing in a more lateral direction, the cornua being thus slightly sigmoidally bent (fig. 85; pl. 76).

The cornua are rather short in *Cephalaspis eurynotus* (fig. 44; pl. 18:2) and very short in an undetermined *Cephalaspis* species (pl. 55:2). In the genus *Boreaspis* they are generally long or very long but short in *B. intermedia* (fig. 89; pl. 88) and very short in *B. robusta* (fig. 86; pls. 78:3; 79; 80), *B. puella* (fig. 87; pls. 82—83) and *B. costata* (fig. 88; pl. 84:2; 85, *c;* 86:2; 87:1). Also in *Kiaeraspis* the cornua are very short (fig. 100; pl. 97:1,3; Stensiö 1927, figs. 3—5, 79; pls. 51—53; 55—56; 58), and in *Axinaspis* (fig. 101; pls. 97:4; 98:2; 100:1), *Acrotomaspis* (figs. 102—103; pls. 101:1; 104:3-4; 105) as well as in *Nectaspis* (figs. 104—106; pls. 106—108; 110:2; 111; 112:2; 113:1,3) they are absent, being replaced by a more or less obtuse lateral angle on the shield. In *Axinaspis* and *Acrotomaspis,* at least, we can assume that this non-development of the cornua is the result of a regressive development from a more primitive stage with better developed cornua, as exhibited in *Kiaeraspis.*

The shape of the cornua is also very variable (as is seen in the systematic descriptions). In some *Cephalaspis* species they are extremely large, broad and flattened and constitute in fact a major part of the cephalic shield (see e. g. figs. 64—71; pls. 48; 50; 52—54; 55:1).

In cross-section the cornua are generally somewhat flattened, but are almost circular in some species, as in *Cephalaspis verruculosa* (pl. 24) and *C. tenuicornis* (pls. 26:1; 27:2). In most species of the genus *Cephalaspis* they are provided along their dorso-medial margin with a narrow border, formed by the exoskeleton (limbus cornualis, fig. 5A—B, *lb).* The margin of this border is in some species even (pls. 48:3; 49:2), in others provided with minute and scattered denticles (pls. 50:1; 55:1, *lb;* cf. also pl. 5:2) or with closely set, hooke-like denticles (e. g. fig. 5A; pls. 5:6; 9:4; 10:2; 11:3, 5). These latter are the real denticles (denticuli cornuales), which thus invariably are to be found as tooth- or hook-like projections on the cornual limb. In some species the whole outer face of the exoskeleton of the cephalic shield is ornamented with high tooth-like tubercles, and these tubercles thus also occur on the inner side of the cornua; they should not be confounded with the real denticles (cf. *C. powriei,* p. 318 and *C. arcticus,* p. 343).

The cornual border, just mentioned, in general gradually narrows anteriorly and disappears (pl. 52), but in some species it ends rather abruptly (pl. 55:1), and there is thus formed an obtuse angle on the medial side of the cornua (this angle seems in some specimens to have come into existence through the border being broken, cf. p. 421; Stensiö 1927, pl. 2:4); this is evidently what has been called the pectoral or medial angle of the cornu (Stensiö 1927, p. 26; fig. 1; cf. pls. 1:3; 2:3-4; 11), it has not been found to have any relation to the extent of the articular area of the shoulder-girdle (cf. Stensiö 1927, p. 26).

The pectoral sinus, a posterior recess in each zonal part, is in general well defined when the cornua are well developed, but ill defined when the cornua are short (as e. g. in *Kiaeraspis).* In *Axinaspis* and *Acrotomaspis* the pectoral sinus is absent, and in *Nectaspis,* it probably forms only a very shallow concavity in the postero-lateral side of the shield.

In some species with well defined pectoral sinus, the posterior wall of the shoulder-girdle, besides being concave, stands somewhat obliquely in such a way that its dorsal margin lies more posteriorly than its ventral margin (see e. g. *Cephalaspis* sp., pl. 55:2; *Benneviaspis holtedahli,* fig. 5C; pl. 71:1; cf. *C. exilis? ("C. hoeli")* Stensiö 1927, pl. 99); in ventral view the pectoral sinus is thus somewhat deeper than in dorsal view. In describing *Cephalaspis kozlowskii* Zych (1937, p. 65) has assumed that the pectoral fin "lay fairly low, a condition which may mean that during swimming or other movements of the animal it could easily be directed downward"; although the fact on which Zych based his assumption (the low position of the openings for the vessels to the pectoral fin) is not universal in *Cephalaspis,* we can, because of the oblique position of the posterior wall of the shoulder-girdle in some species, suppose that the fin in these forms was much more movable in a ventral than in a dorsal direction. In *Cephalaspis ibex* (fig. 18; pl. 28:2) the dorsal and ventral margins of the middle part of the zonal part reach backwards to about the same distance.

The extent of that surface on the shoulder-girdle, to which the pectoral fin was attached (here called the pectoral area, or the attachment area for the pectoral fin), and which is lined with a membrane of the external layer of the endoskeleton but, of course, devoid of exoskeleton, is demarcated on fig. 18A; we find that it reaches from the medial side of the zonal part at the transition to the interzonal part on to the antero-medial side of the cornu. The basis of the pectoral fin must thus have been fairly broad.

When clearing out the pectoral sinus in a *Cephalaspis* specimen, we find that the posterior wall of the shoulder-girdle, that is the pectoral area, is never wholly complete, being more or less imperfectly preserved. It looks as if the pectoral fin, on becoming detached from the cephalic shield after the death of the animal, has torn asunder the thin perichondrial bone membrane lining the large muscle fossa and often also surrounding parts of the shoulder-girdle. The best preserved shoulder-girdle is found in a specimen of *C. ibex* (fig. 18; pl. 28:2); another less well preserved is exposed in *C. signata* (pl. 30:2).

The pectoral area of the shoulder-girdle is pierced by many canals, which will be considered in more detail in the remarks upon the endo-

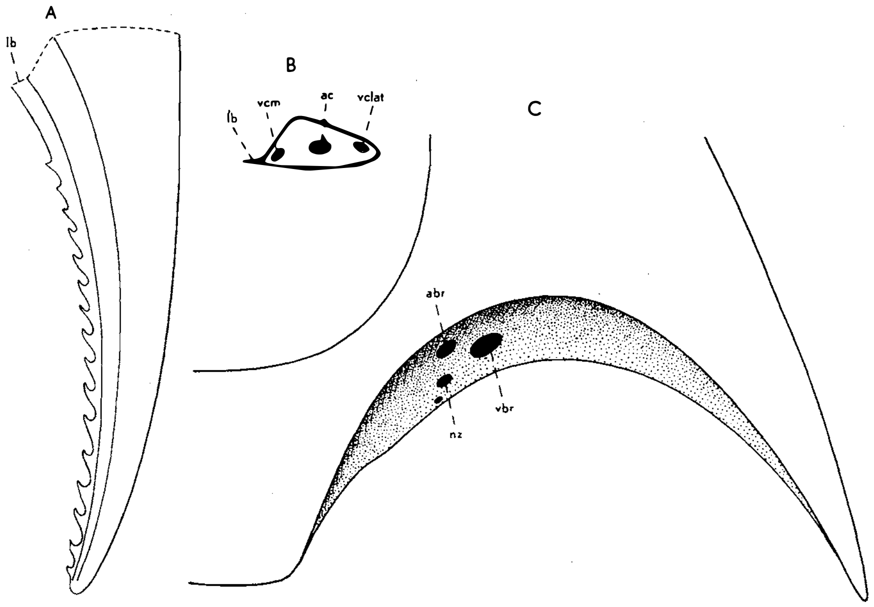

Fig. 5. — A, B, left cornu of *Cephalaspis vogti,* A, in ventral view, B, in cross-section; C, zonal part of the left side of the cephalic shield in *Benneviaspis holtedahli,* ventral view. × 4.

abr, opening of canal for the a. brachialis; *ac,* canal for the a. cornualis; *lb,* exoskeletal cornual limb; *nz,* opening of canal, probably for a nerve; *vbr,* opening of canal for the v. brachialis; *vclat,* canal for the v. cornualis lateralis; *vcm,* canal for the v. cornualis medialis.

skeletal shoulder-girdle. We will here only say a few words on the appearance of the face of the pectoral area.

The surface of the pectoral area is not quite smooth but provided with usually rather indistinct ridges and depressions. We find thus in *C. ibex* a transverse ridge or low crest in the upper part of the vertical wall dorsally to the opening vbr_1 (in *C. signata* the ridge reaches somewhat dorso-laterally to this opening), extending in medial direction to a point just ventro-laterally to the opening *nz* from which it turns for a short distance in ventro-medial direction and disappears. It borders a large and probably deep fossa on its dorsal and dorso-medial sides, between the openings vbr_1 and *nz*. This fossa I regard as a muscle fossa, the attachment area for a powerful muscle of the pectoral fin. From the opening *nz* there extends a rather short and indistinct ridge in medial direction, and, ventrally to it, there is a transverse, very faintly developed depression. There is furthermore a ridge between the openings *abr* and vbr_2 and a very shallow depression from the opening vbr_1 running in latero-posterior direction (on the antero-medial side of the cornu; see fig. 18B). The significance of all these small irregularities on the surface of the pectoral area cannot be explained without knowing anything of the endoskeleton of the pectoral fin. We can, however, note that there is no special, distinct or well defined, space within the pectoral area, which can be interpreted as an articular area for the pectoral fin.

In such forms as *Axinaspis, Acrotomaspis* and *Nectaspis,* in which no real pectoral sinus are developed, an anterior part of the postero-lateral sides of the cephalic shield, or of the zonal parts, is developed into a pectoral area, an attachment area for the pectoral fin. This area is known in detail only in *Axinaspis* (fig. 19; pl. 98:3); in *Acrotomaspis* and probably also in *Nectaspis* it seems on the whole to be similary developed and occupies in these forms a very shallow *(Acrotomaspis)* or a shallow, but fairly distinct, depression in the postero-lateral vertical wall of the zonal part.

In *Axinaspis* (fig. 19; pl. 98:3) the pectoral area forms an oblong space on the vertical postero-lateral wall of the shield from the lateral angle of the shield and backwards to a point at about three-quarters of the distance between this lateral angle and the postero-lateral angle of the inter-zonal part. The area is broadest in its anterior half and here retains its breadth for some distance; in the posterior half it gradually narrows towards the posterior end, which lies at the dorsal margin of the vertical wall of the zonal part. A fairly broad, almost vertical ridge separates an anterior rather deep fossa from the rest of the area. From the ventral part of this ridge there run two well marked, rather sharp-edged ridges in posterior direction, one of them, which proceeds postero-dorsally, forming the ventro-lateral boundary of a triangular antero-dorsal depression; the other, which is rather indistinct anteriorly and runs in almost straight posterior direction, turns soon somewhat dorsally and becomes more sharp-edged with abrupt ventral slope; coming to the posterior fourth of the area, it gives off a short postero-ventrally directed branchlet, which is placed at right angles to the main ridge. This ridge continues in the original direction for only a short distance sloping downwards, and ends at an opening *(x)* of unknown significance. Ventrally to the main ridge and antero-ventrally to its postero-ventrally directed branch there is formed a narrowly triangular recess or shelf. The middle part of the area between these two longitudinal ridges is fairly even with two very indistinct depressions near the first ridge. Most posteriorly in the pectoral area there is an oblong shallow depression along the postero-ventral margin of the area.

In *Axinaspis* too, it is impossible to explain the significance of all these irregularities on the surface of the pectoral area. It can be assumed that the more pronounced depressions are the attachment areas of muscles for the pectoral fin. The most anterior rather deep fossa is thus conceivably the muscle fossa of a rather strong abductor, and the triangular shelf in the postero-ventral part of the area the fossa of a depressor muscle.

The inter-zonal part of the cephalic shield varies rather much in shape and in its backward extension. In *Kiaeraspis* it is often very long, and is assumed to have been formed by 10 or 11 body segments (Stensiö 1932, pp. 8—9), so many rows of trunk-scales being included in the inter-zonal part. This part of the shield is furthermore fairly long in *Axinaspis* and somewhat shorter in *Acrotomaspis*. In *Nectaspis* it is not very much extended, and in *Cephalaspis* the backward extension of the inter-zonal part varies considerably. It is thus e. g. very short in *C. doryphorus* (fig. 55; pl. 40) and fairly long in *C. signata* (fig. 51; pls. 28:1; 29:1), in which the dorso-posterior portion is rather much produced backwards. The inter-zonal part of the shield is short in *Ectinaspis, Benneviaspis, Hoelaspis* and *Boreaspis*.

As observed by Stensiö (1927, p. 25; 1932, p. 9) and Heintz (1939, p. 11) the number of transverse rows of trunk-scales included in the inter-zonal part is greater in the dorsal half than in the ventral half.

In *Cephalaspis pinnifera* (pls. 42; 43:2) it is obvious that parts of the dorsal halves of nine rows of trunk-scales are included in the postero-dorsal portion of the inter-zonal part (the dorsal spine included). Besides these rows we can without doubt count one more, and probably expect the existence of at least two additional ones, of which, however, no external vestiges are left. In this species, which has a rather short but in its dorsal portion somewhat produced inter-zonal part with a small dorsal spine, we thus find that the number of transverse scale-rows included in the inter-zonal part of the cephalic shield, and accordingly the number of trunk-segments composing that part, must be at least 12.

The extension and the general shape of the inter-zonal part is not only dependent on the number of composing trunk-segments but also on the size of these segments, their disposition and how large a part of each of them is included in the inter-zonal part.

The inter-zonal part is in most forms provided with a dorsal median longitudinal ridge, which in some species is produced posteriorly into a spine of very varying length and shape. This spine is thought by Kiær (1911, p. 16) and Stensiö (1927, p. 26) to form the vestige of a reduced anterior dorsal fin, and evidently considered by Stensiö (1932, p. 68) to form an anterior continuation of the dorsal fin-fold, represented by the dorsal crest. This latter interpretation seems very likely, and the spine (and the median ridge) must thus, at least partly, have been formed by transformed and rigidly connected unpaired scales, homologous to the scutes of the dorsal crest; no vestiges of such scales are, however, seen in the Spitsbergen Cephalaspids.

The basal part of the spine is somewhat or distinctly broader than the distal part (this is most evident posteriorly), and there is formed a socle-like basis of the spine, which is triangular in cross-section or seen from behind (fig. 6); this part between the main cephalic shield and the shaft of the spine is here simply called the spinal base *(bdsp).* In lateral view there is seen a more or less distinct angle on the posterior margin of the spine at the transition between the spinal base and the distal part of the spine. This angle is called the postero-ventral angle of the dorsal spine *(pvdsp,* fig. 6; pls. 28:3; 34:2; 35:1-2). When the cephalic shield is viewed from behind, we find that the posterior wall of the spinal base is not covered by exoskeleton but that there is formed a triangular ventrally open emargination in the base, which thus has the appearance of being saddle-like with a central cavity (fig. 6, to the right); this basal cavity is generally filled with the inter-zonal endoskeleton (which also to a varying length reaches up into the shaft of the spine; see further p. 54).

These features in the dorsal spine can only be explained if we assume that the dorsal crest of the scale-covered trunk division lay immediately behind the dorsal spine, and that its most anterior scute fitted into the posterior wall of the spinal base and articulated with this base (in about the same way as the scutes of the dorsal crest between themselves). No real articular facets have, however, been observed on the dorsal spine (the specimens are not sufficiently well preserved in these parts of the spine), but in *C. oreas* the exoskeleton is seen to reach slightly behind the endoskeleton. The resulting free borders of the exoskeleton possibly overlapped a part of the anterior margin of the foremost scute.

The conditions, referred to above, thus also indicate that the dorsal spine is to be regarded as an anterior, transformed and enlarged part of the dorsal fin fold.

With regard to the different shape of the dorsal median ridge and the dorsal spine, it can be noted that the dorsal median ridge is very short but fairly distinct in some *Cephalaspis* species (see e. g. pl. 9:5, *dr*), while in other species of the same genus it is rather low, fairly long and sharp-edged (pls. 2:2; 6:1; 48:1; 49:1). The same development is seen also in the genera *Securiaspis* (pl. 61), *Tegaspis* (pls. 65:1; 66), *Axinaspis* (pl. 100:3), *Acrotomaspis* (pls. 101; 102:1) and *Nectaspis* (pl. 111:3-4). In some *Cephalaspis* species the dorsal median ridge forms a rather thick low crest (fig. 40; pls. 12:2; 19:1). Often the ridge rises somewhat posteriorly and thus forms a low and rather short dorsal spine (pls. 42; 43:2, *dsp*) or is somewhat produced in postero-dorsal direction, forming a backwardly inclined dorsal spine (figs. 31, 34, 48, 59). This spine can be shaped as a fairly high crest with somewhat truncate (fig. 25) or acuminately produced apex (fig. 47). The spine is sometimes erect and fairly long (pls. 56:3; 59:2) or, in some

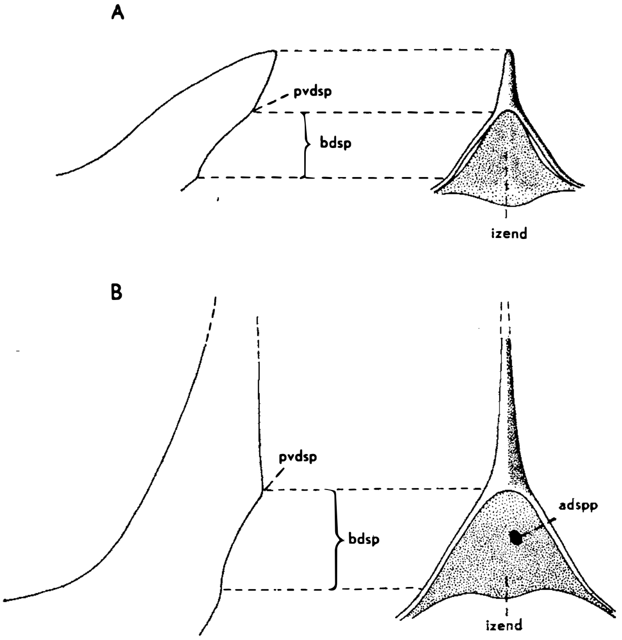

Fig. 6. — Dorsal spine on the inter-zonal part of the cephalic shield, A, in *Cephalaspis oreas,* B, in *Cephalaspis doryphorus,* seen in lateral view (to the left) and from behind (to the right). A, × 4; B, × 3.

adspp, opening of the canal for a posterior a. spinae dorsalis; *bdsp,* spinal base; *izend,* inter-zonal endoskeleton; *pvdsp,* postero-ventral angle of the dorsal spine.

species, extremely long and vertical (figs. 52—53, 55; pls. 34:2; 35:1; 40:1-2) or even somewhat forwardly inclined (fig. 54; pl. 35:2). In the following genera no dorsal median ridge is developed at all, viz. in *Ectinaspis* (pl. 67:2), *Benneviaspis* (e. g. pl. 70:2), *Hoelaspis* (pls. 76; 77:2) and *Boreaspis* (see pls. 78:3; 79:1; 80; 88:1-3, 5; 90:1, 5; 95).

In the genera *Benneviaspis, Hoelaspis* and *Boreaspis* the posterior margin of the dorsal portion of the inter-zonal part is distinctly emarginate between the postero-lateral and the posterior angles; there is thus formed a characteristic paired posterior sinus in the dorsal roof of the inter-zonal part, the sinus inter-zonalis (dorsalis), the (dorsal) inter-zonal sinus (figs. 77—99; pls. 68:2-3; 69; 70:2; 71:1; 73; 75:1; 76; 77:2; 78:1, 3; 79; 80; 82:2-4; 88:1-3, 5; 89:4, 6; 90:1-2, 4-5; 92; 95; 96).

The cavity in the posterior part of the shield behind the postbranchial wall and which is bordered dorsally by the roof of the inter-zonal part, laterally by the lateral walls of this part and a postero-median portion of the zonal parts and ventrally by the floor or ventral portion of the inter-zonal part (when present) and open backwards is referred to as the trunk cavity of the cephalic shield. This cavity is very deep when the inter-zonal part of the shield is long, as in *Kiaeraspis,* and very shallow when this part is short, as in *Benneviaspis* and others; it is generally more or less open ventrally as the inter-zonal part is much shorter ventrally than dorsally.

For the sake of convenience the ventral floor of the inter-zonal part is thought to extend forwards on to the oralo-branchial fenestra, although by definition a narrow zone along the posterior border of the fenestra belongs to the cephalic shield proper (Stensiö 1927, p. 20).

The inter-zonal part is, as far as observed, complete ventrally in all the Spitsbergen Cephalaspids, except in *Nectaspis,* in which it forms on each side a ventro-medially pointed process, which does not meet its fellow of the other side, but leaves a median gap in the exoskeleton (fig. 105D). This gap lies immediately below the ventral notch in the endoskeletal post-branchial wall, which transmitted the truncus arteriosus.

In *Axinaspis* and *Acrotomaspis* the inter-zonal part can be said to form three different, fairly well separated portions, a dorsal, horizontal roof, which, as mentioned above, is rather long, the paired vertical lateral wall, which decreases in breadth in ventral direction, and in *Acrotomaspis* (fig. 102C; pl. 104:1-2) in its ventral half only consists of two narrow bars, forming the connection to the third portion or the ventral, horizontal floor, which anteriorly is produced as a median process into the oralo-branchial fenestra (figs. 101C, 102D; pls. 99:1; 104:1-2).

Exoskeleton of the cephalic shield.

In this section I shall deal briefly with the different modifications in the minute structure of the exoskeleton in the cephalic shield in the Spitsbergen Cephalaspids.

The fundamental characteristics of the exoskeleton in the Osteostraci have been elucidated by the investigations of Stensiö (1927, and mainly 1932) and in this respect nothing essential can be added in studying the Spitsbergen forms. As already pointed out by Stensiö (1927, p. 32) the exoskeleton of the Spitsbergen Cephalaspids is in general but little suitable for examination of its minute structure, and this structure can be understood clearly only in the light of the conditions in the well preserved forms from Great Britain.

Before proceeding I shall give a short recapitulation of the principal microanatomical features of the exoskeleton in the Osteostraci (see fig. 7, which schematically reproduces the conditions in a rather normal cephalaspid form).

When completely developed the exoskeleton consists of three different layers, the basal, the middle and the superficial layers. The basal layer *(bl),* composed of regular horizontal lamellae, is comparatively solidly built and encloses rather few canals; basally it contains parts of the subcutaneous vascular canal plexus *(dplx).* At its bottom the middle layer *(ml)* passes gradually into the basal layer and peripherally into the superficial layer; it contains numerous canals so that it often

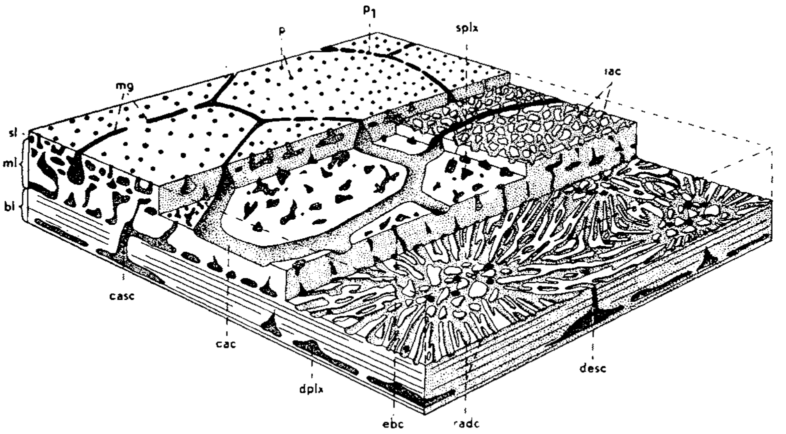

Fig. 7. — Schematic block diagram of the exoskeleton in the cephalic shield of *Cephalaspis excellens.*

bl, basal layer; *cac,* circum-areal mucous canal; *casc,* ascending vascular canal; *desc,* descending vascular canal; *dplx,* subcutaneous vascular canal plexus; *ebc,* external branches from the ascending and radiating vascular canals, forming the subepidermal vascular canal plexus; *iac,* intra-areal mucous canals; *mg,* partly covered groove of the mucous canal system; *ml,* middle layer; p, p_1, pores of the mucous canal system; *radc,* radiating vascular canals; *sl,* superficial layer; *splx,* subepidermal vascular canal plexus.

only consists of thin trabeculae. The canals in the middle layer belong to two different systems, viz. the mucous canal system, mainly situated in the outer division of the layer, and the canals of the vascular system, which chiefly occupies a lower division in this layer. The superficial layer *(sl),* which generally is very thin, consists of dentine (most superficially enamel-like); it forms a covering to the middle layer and is pierced by fairly wide pores *(p)* or grooves *(mg)* of the mucous canal system.

The mucous canal system consists of a network of horizontal canals, and among these we can in many forms distinguish between rather wide, circum-areal canals *(cac,* Gross 1935, "inter-areal canals", Stensiö), which subdivide the outer division of the middle layer into polygonal areas, and canals of a fine calibre, the intra-areal canals *(iac),* which form a fine-meshed network within the polygonal areas, and which are in communication with the circum-areal canals. Both the circum-areal and the intra-areal canals open to the exterior, the latter through ascending so-called pore canals (Gross) which pierce the superficial layer by the pores *(p),* mentioned above, and the former through pores (p_1) or short or long slit-like openings. In this latter case the canals are thus more or less covered grooves *(mg).* Denison (1947, cf. 1951b) has, after an examination of the exoskeleton of *Tremataspis,* described the mucous canals ("sensory canals") in this genus as being divided by a horizontal septum into an outer and an inner division (Denison 1947, pp. 341—342, 352—353; figs. 1, 3, 5—6, 9, 11;

pl. 2:1-2; 1951b, fig. 32A). As far I can see the lower division of the canals must be canals of the horizontal submucous vascular plexus (Wängsjö 1944, p. 357; fig. 5; pl. 7:2; cf. Denison 1951b, p. 208; figs. 32B, 35A).

The vascular canals start from the subcutaneous vascular canal plexus *(dplx)*. From this plexus issue groups of ascending vascular canals *(casc)*, in general one group towards the center of each polygonal area. They thus pierce the basal layer in centrifugal direction, and, arriving in the lower division of the middle layer, branch into horizontal, radiating canals *(radc)*, which run to the periphery of the polygonal area below the circum-areal canals of the mucous canal system, where they meet corresponding canals from the adjacent polygonal areas. From the peripheral parts of the radiating canals issue descending vascular canals *(desc)*, which run in centripetal direction through the basal layer to the canals of the subcutaneous vascular plexus or, in some forms, to rather wide canals, ringsinus, in the basal division of the basal layer. These ringsinus form a wide-meshed network in which the canals lie conformably below the circum-areal canals of the mucous canal system. Through the disposition of the vascular canals vascular areas are formed in the exoskeleton, which topographically correspond in size and shape to the polygonal areas. From the ascending and the radiating vascular canals there issue small external branches *(ebc)* to the outer division of the middle layer, and these canals form here, below the intra-areal mucous canals, a subepidermal vascular canal plexus *(splx)*. From this plexus emanate small external branches which pass over into the dentine canals of the superficial layer. In addition small canals connect the subepidermal plexus with the mucous canals.

The generalized picture of the minute structure of the exoskeleton, given above, is for the most part to be recognized in *Cephalaspis excellens* (fig. 7; pls. 11:1-2; 12:1; 40:4-5; 65:3; 115:2-3).

With a partial non-development of the exoskeleton, the superficial and subsequently the middle layers are reduced to a greater or lesser degree. When the superficial layer is absent, the circum-areal and the intra-areal mucous canals are developed as open grooves, and when also parts of the middle layer are reduced, the intra-areal and eventually also the circum-areal grooves disappear; in these cases the mucous system was situated partly or wholly in the soft tissue outside of the exoskeleton.

Turning now to the structure of the exoskeleton in the Spitsbergen Cephalaspids, we find that the superficial layer of the exoskeleton in very many *Cephalaspis* species is developed as a continuous covering to the middle layer, e. g. in *C. excellens* (fig. 7; pls. 12:1; 115:2-3), *C. recticornis* (pls. 20:1; 114:3) and others; it seems furthermore to be continuous in *Benneviaspis, Hoelaspis, Boreaspis* (pl. 117:2-3), *Kiaeraspis, Axinaspis* (pl. 116:2), *Nectaspis* (pl. 118:3), generally so in *Acrotomaspis* (pl. 118:1-2), and probably in *Ectinaspis* and *Securiaspis.*

The outer face of the superficial layer is as a rule quite smooth without any ornament, but in some forms tubercles of different size and shape occur. In species with a smooth outer face in the main parts of the cephalic shield there is a tendency towards a coarse surface through the development of tubercles or ridges in some places, as on the circum-orbital ridge, the antorbital prominence, the borders of the dorsal sensory field, the median dorsal ridge, the rostral and lateral margins of the main shield and the distal parts of the cornua, as e. g. in *C. excellens* (pls. 12:1-2; 40:4-5; 115:3; cf. fig. 40) and *C. recticornis* (pl. 20:1). In some species the tubercles are only low (though sometimes large) and not well defined elevations on the outer face of the exoskeleton (as in *C. recticornis,* pl. 114:3). In others they are well defined (e. g. *C. verruculosa,* pls. 23:2; 114:2), and in *Acrotomaspis instabilis* they are in comparison exceptionally high (pls. 101:2; 103:3; 118:1-2). The tubercles in these species, as well as in *Axinaspis* (pls. 116:2; 117:1) and some others are formed mainly by a strong development of the middle layer, but on the rostral margin of the shield in *C. excellens* (pl. 115:3) the tubercles (and ridges) are thickenings of the superficial layer.

In a few *Cephalaspis* species with a continuous superficial layer this layer is subdivided into polygonal areas by the circum-areal grooves of the mucous canal system, as in *C. aarhusi, C. pinnifera* (pl. 43:2, *par), C. metopias* (pl. 41:1) and *C. gigas,* in the middle and posterior parts of the shield in *C. excellens* (pls. 11:2; 12:2; 14).

The superficial layer is discontinuous (and if so most often also an outer part of the middle layer is missing) and only present in the tubercles in *C. deltoides, C. verruculosa* (pl. 114:2), *C. signata, C. jarviki* and others, as well as in *Tegaspis* (pl. 116:1).

In some species the superficial layer of the exoskeleton is variably developed in different specimens *(C. exilis)* or even in different parts of the shield in one specimen *(C. powriei,* cf. also *C. vogti).*

As to the general development of the middle and the basal layer not much is to be said. Part of the middle layer is absent when the superficial layer is discontinuous, but most of the lower division seems always to be present. The lower division of the middle layer is very thin in *Benneviaspis, Hoelaspis* and *Boreaspis* (pl. 117:2-3), but in some species of *Cephalaspis* (pl. 115:1) the same division is exceptionally thick. This different development is due to a weak or strong development of the horizontal vascular canals (radiating canals) in this division.

The basal layer is more strongly developed and thicker in the posterior portion of the cephalic shield, on the inter-zonal part, where it is not underlain by endoskeleton (cf. *Dartmuthia,* Wängsjö 1944, pp. 350—352) than in other parts of the shield.

When the superficial layer is present and continuous the mucous canal system is enclosed in the exoskeleton (Stensiö 1932, p. 19). It is distinctly differentiated into wide circum-areal and narrow intra-areal canals in *C. excellens* (fig. 7; pls. 11:1-2; 115:2), *C. vogti, C. broughi, C. menoides* and partly, in *C. dissimulata;* the circum-areal canals are in some places (mostly in the posterior part of the shield) developed as more or less covered grooves (in *C. excellens, C. vogti, C. pinnifera).* In *C. aarhusi, C. metopias* (pl. 41:1), *C. gigas* as well as in *Securiaspis staxrudi* (pls. 63:1; 65:2) there are open circum-areal grooves and closed intra-areal canals. In *Securiaspis staxrudi* (pl. 65:2) we find that in the anterior part of the shield the circum-areal grooves are arranged into three or four concentric grooves while in the inter-zonal part the circum-areal grooves are in general simple and undivided; the conditions here thus remind of those in a *Cephalaspis* species, figured by Stensiö (1932, fig. 5B, C).

With non-development of the outer parts of the exoskeleton, the mucous canal system is only partly enclosed in it and lodged in open grooves. In some species, as *C. signata* (pls. 28:1; 114:1), *C. ibex, C. corystis* and others we can distinguish between circum-areal and intra-areal grooves. In *C. jarviki* and *C. lanternaria* (pl. 54) and in *Tegaspis* exist circum-areal grooves but no intra-areal grooves have been observed (probably the intra-areal parts of the mucous system lay entirely outside of the exoskeleton). In *C? pedata* the outer parts of the exoskeleton are in some places subdivided into polygonal areas through broad circum-areal grooves, in other places there is formed a wide-meshed and very irregular network of wide and narrow grooves, encircling low elevations or tubercles (pl. 68:1), in which narrow intra-areal canals are developed; the grooves must have partly lodged circum-areal or modified circum-areal divisions of the mucous system.

In very many Cephalaspids, and thus in many *Cephalaspis* species, as in *C. oreas, C. heintzi, C. hoeli, C. hyperboreus, C. eurynotus, C. recticornis* (pl. 114:3), *C. curta* and others (pl. 115:1), in *Ectinaspis, Benneviaspis, Hoelaspis* (pl. 77:1), *Boreaspis* (pl. 117:2-3), *Axinaspis* (pls. 116:2; 117:1), *Acrotomaspis* (pl. 118:1-2), *Nectaspis* (pl. 118:3) and probably in some *Securiaspis* species and in *Kiaeraspis* the mucous canal system is developed as a uniform, fine-meshed network of canals, in which no differentiation between circum-areal and intra-areal canals can be observed. In *C. fracticornis* the mucous canal system is partly developed as a network of canals, partly as a network of open grooves (pl. 47:1).

In *Cephalaspis* the vascular canal system of the middle layer generally shows well developed radiating canals, mostly forming definite vascular areas, as in *C. excellens* (fig. 7; pls. 11:2; 65:3). In this species, however, there is formed in the middle of each polygonal area a fairly wide plexus of anastomosing horizontal canals from which the comparatively short radiating canals issue. In *C. eurynotus* (pl. 21:2) and *C. recticornis* (pl. 21:3) the radiating canals are very irregular and of varying calibre. The radiating canals of some of the species from the Wood Bay series (as *C. jarviki, C. oblonga, C. semicircularis, C. menoides)* are extremely narrow.

Radiating canals are, besides in *Cephalaspis,* developed also in the genera *Securiaspis, Tegaspis* (pl. 65:1), *Ectinaspis, Kiaeraspis, Axinaspis* (with irregular vascular areas), *Acrotomaspis* and *Nectaspis.*

Generally there is only one layer of radiating canals (fig. 7; pls. 114:2-3; 115:2; 118) but in an undeterminable specimen of *Cephalaspis* (pl. 115:1) four or five layers of radiating canals are observed, as in *Hemicyclaspis murchisoni* (Stensiö 1932, fig. 7; pl. 60). The interrelations between these layers could not be worked out.

In the genera *Benneviaspis, Hoelaspis* and *Boreaspis* the horizontal vascular canals in the thin inner division of the middle layer (or the submucous vascular canals, cf. Wängsjö 1944, p. 357, in reference to *Tremataspis),* are not developed as radiating canals but consist, in the main parts of the shield, of a single layer of anastomosing canals, forming a fine-meshed network (pl. 117:2-3).

In the basal layer regular ringsinus have been observed in the major part of the cephalic shield in but a few species, as *C. aarhusi* (pl. 1:1), *C. tenuicornis* (pl. 26:1), *C. metopias* (pl. 41:2), *C. gigas, C. lanternaria,* an indeterminable *Cephalaspis* specimen (pl. 55:1), and in *Tegaspis* (pls. 65:1; 66), forming polygonal areas in the basal layer (pl. 65:1, *par).* In other species *(C. acuminata, C. vogti, C. arcticus, C. pinnifera, Securiaspis staxrudi* (p. 61), *Ectinaspis heintzi* (ringsinus, often irregularly developed and not forming distinct polygonal areas, are observed in the inter-zonal part, and mostly in the posterior portion of this part. In *C. broughi, C. deltoides* and a few others the lower part of the basal layer contains irregular horizontal canals, which probably correspond to the ringsinus, but which do not form polygonal areas. In most of the *Cephalaspis* species, as well as in the genera *Benneviaspis, Hoelaspis, Boreaspis, Kiaeraspis, Axinaspis, Acrotomaspis* and *Nectaspis* no ringsinus have been observed.

In certain parts of the cephalic shield there are seen some discrepancies in the disposition of the mucous and vascular canals from the normal conditions. Along the anterior and lateral margin of the shield the superficial layer in *Cephalaspis excellens* is ornamented with long or short longitudinal ridges (pls. 12:1; 40:5), and between them the mucous canals are situated (pl. 115:3, *mc),* thus forming longitudinal canals; the vascular canals in the middle layer are oriented in a similar way. Similar conditions are met with in *C. oreas, C. hoeli* (pl. 11:3), *C. exilis* (pl. 11:5) and other *Cephalaspis* species as well as in *Securiaspis;* in a few *Boreaspis* species *(B. macrorhynchus, B. curtirostris)* longitudinal vascular canals are observed along the margins of the main shield and *(B. curtirostris)* in a similar way also along the borders of the dorsal sensory field (cf. also the disposition of the vascular canals in *C. powriei,* Stensiö 1932, pls. 63:3; 66:1, *rad. c).* In *C. eurhynchus,* most anteriorly on the dorsal side of the shield, longitudinal vascular canals run forwards, converging towards the apex of the rostrum (pl. 5:6). In *Boreaspis* longitudinal vascular canals run all along the rostral process while the mucous canals form a uniform network as on the main shield (the vascular canals are distinctly seen in pls. 78:2; 80:2). In *C. fracticornis* (pl. 47:1), the middle layer along the margins of the shield is traversed by longitudinal vascular canals *(lvc);* these canals issue from obliquely ascending vascular canals *(casc).*

It has been shown (Stensiö 1932) that there exists a correlation between the disposition of the mucous and the vascular canals in the exoskeleton, the vascular canals being disposed "in vascular areas, which in shape and extent agree with the polygonal areas of the exoskeleton" (Stensiö 1932, p. 73), and "since we know that the subdivision of the exoskeleton of the cephalic shield into polygonal areas is due to the mucous canal system, it follows that the arrangement of the vascular canals into groups — vascular groups — is also determined by the mucous canal system, which is thus a dominant factor in the structure of the exoskeleton" (Stensiö 1932, p. 24). In the Spitsbergen Cephalaspids such a correlation exists in many species. And in the genera *Benneviaspis, Hoelaspis* and *Boreaspis,* in which the mucous canal system is developed mainly as a uniform fine-meshed network and where the underlying, submucous, vascular canals are disposed in a similar manner, we find also a correlation in the disposition of the mucous and vascular canals.

This correlation is, however, not universal and not even of a prevalent occurrence. The most widespread condition in this respect is a combination of a vascular canal system disposed in regular vascular areas, and a mucous canal system present as a uniform net-work, which does not subdivide the exoskeleton into polygonal areas.

In *Tremataspis mammillata* (see Wängsjö 1944, pp. 357—358) we find a combination of irregularly disposed submucous vascular canals (corresponding to the radiating canals in other Osteostraci) and of a net-work of mucous canals (probably corresponding to circumareal canals), forming polygonal areas. In *Dartmuthia* (Wängsjö 1944) there are well defined vascular areas (according to Denison, 1951b, only in the dorsal exoskeleton) but the disposition of the mucous canals is not clearly or not wholly correlated to that of the vascular canals. In *Oeselaspis* we find (Denison 1951b, pp. 206—209) irregularly radiating vascular canals and a fine-meshed net-work of mucous grooves, and in *"Procephalaspis" oeselensis* a combination of normal radiating canals and circum-areal and intra-areal mucous grooves (Denison 1951b, p. 211). We thus find in the oldest known Osteostraci a diversity of combinations with regard to the disposition of the vascular and mucous canals.

The first exoskeleton elements to appear were probably small superficial tubercles or scales (cf. Sewertzoff 1931, p. 31; Gross 1933c, p. 108; Heintz 1939, pp. 103—105; Westoll 1945, pp. 345—346, 351; Obruchev 1945; Ørvig 1951, pp. 366—368). Such superficial tubercles may have been present in the immature stages, and the ossification of the deeper layer of the corium which must have begun in the center of the vascular areas can also have started before the animal was full-grown. As long as the peripheral parts of the vascular areas were unossified these areas behaved as small units in the prospective cephalic shield and could continue their areal growth, but as soon as the ossification had reached the outer parts of the areas and the adjacent areas became anchylosed the areal growth of the vascular areas, and thus also the general growth of the animal, ceased. Through the subdivision of the dermis in vascular areas by means of radiating vessels the prospective shield had a great possibility to grow and increase in size, and the ossification of the dermis could begin before the animal was full-grown. In other forms, as in *Tremataspis* and others, in which the vascular canals are not disposed as radiating canals and the dermis was not subdivided into separate areas, no growth could occur after ossification had set in. This is substantiated by the observations of Denison (1947) on the development of the exoskeleton. The structure of the dermis in *Tremataspis* and others (*Benneviaspis* and allies) was most certainly secondary (cf. Obruchev 1945, p. 267).

Thus it seems that the disposition of the vessels in the dermis was a dominant factor for its structure and consequently also for the structure and development of the exoskeleton.

The minute structure of the plates of the sensory fields (which are found in *Cephalaspis pinnifera* and *Tegaspis kolleri)* corresponds in the main to that of the rest of the exoskeleton (as in *Hemicyclaspis murchisoni* and *C. pagei,* Stensiö 1932, p. 26; cf. also *Tremataspis,* Denison 1947, p. 356), and thus the plates consist of exoskeleton only.

The plates are independent units of the exoskeleton; they are thus generally wholly separated from each other and from the rest of the cephalic shield (cf. Denison 1947, fig. 10B; also observed by me on sections through the lateral fields of *Tremataspis);* in some cases, however, the plates are anchylosed to each other (cf. Stensiö 1932, pl. 32:1), being separated only by sutures, or to the rest of the cephalic shield (cf. p. 29; pl. 116:1). In many cases this is apparently the cause of the plates being preserved and found in position.

In the two Spitsbergen species *(C. pinnifera, Teg. kolleri)* each plate corresponds in shape and extent and in the relations of its vascular and mucous canals ordinarily to a polygonal area on the rest of the cephalic shield; the circum-areal grooves or canals of the mucous system in these fields must have been situated between adjacent plates.

The main difference between the minute structure of the plates of the sensory fields and the exoskeleton on the rest of the shield lies in the development of the basal layer, which in the former contains cavities in its inner parts. Between the endoskeleton and the plates in *Tegaspis* there is thus formed a wide but rather low cavity, which, through partitions from the basal layer of the plate, is partly subdivided into separate chambers (pl. 116:1, *bch)* or, expressed in other words, between the basal parts of the basal layer of the plate and the endoskeleton is a narrow vacuity and from it extend rather shallow separate cavities up into the middle parts of the basal layer of the plate. The basal cavities in the plates are not closed chambers but are in open communication with the exterior through the open gaps between the plates and between them and the borders of the fields.

In this connection can be mentioned that the plates in *Tremataspis* (which I have examined in a specimen of *T. mammillata)* consist of the superficial, the middle and the outer parts of the basal layer, and that they are separated by a small gap in the middle parts of the basal layer from the underlying part of the shield, to which thus the basal parts of the basal layer are adhering. (The space between the plate and the underlying part of the shield seemingly is not situated between the basal layer of the exoskeleton and the endoskeleton, as maintained by Denison 1947, p. 356, and as in *Tegaspis,* described above.) It can also be observed that the plates of the sensory fields in *Tremataspis mammillata* are much larger than the polygonal areas formed by the mucous canals, and that each plate encloses several such areas.

The significance of the above-mentioned conditions in the sensory fields will be discussed later (p. 193).

Yet another matter is to be considered with regard to the exoskeleton, viz. the relation of the sensory line system to the exoskeleton.

This system is not very easily observed in the fossil Cephalaspids, in which it is represented by open grooves in the exoskeleton. These grooves were thought by Stensiö (1927, p. 235; 1932, p. 48) to lie very superficially and be present in general only when the outer parts of the exoskeleton were well developed. Denison (1947, pp. 350; 1951b; cf. Bölau 1951) has, however, shown that in *Tremataspis* and others the sensory lines are situated in the mucous canal system. (From this fact he has drawn the unwarranted conclusion that this latter system must have contained sensory organs with the same function as the sensory lines,[1] a conclusion which has already been criticized by Robertson 1950, pp. 342—344.) I can on the whole confirm the facts brought forward by Denison, but must add that the canals or the partly covered grooves for the sensory lines in *Tremataspis* even in superficial view (when the outer parts of the exoskeleton are made transparent with e. g. xylol) can be distinguished from the normal mucous canals by their in general distinctly greater breadth and that in cross-section they are often discerned by being cordate in outline, while a section through a mucous canal and its pore-canal is pyriform in outline. As is seen from the figures by Denison (1951b, fig. 37) the canals for the sensory lines in other forms can often be distinguished from the mucous canals by their greater breadth. These differences alone make it more than probable that the canals (or grooves) in question are different in nature from the normal mucous canals.

In *Dartmuthia* the sensory lines (I have only observed the infraorbital line) are situated in partly covered grooves, which in superficial view, exclusively by their forming a continuous characteristic line, can be distinguished from interstitial mucous canals (cf. Denison 1951b, pp. 205—206).

The sensory lines in *Tremataspis* and *Dartmuthia* lie thus fairly deep in the exoskeleton. The same must be the case to a still higher degree in *Didymaspis* and *Thyestes (T. verrucosus),* for in both these genera the sensory lines are represented by grooves in the exoskeleton. For *Didymaspis* we know (Stensiö 1932, pp. 15, 174) that in the anterior part of the shield only the basal layer is present in the intertubercular spaces. In *Thyestes verrucosus* (cf. Stensiö 1932, pp. 15, 164, 169; Denison 1951b, pp. 209—210) only the basal part of the lower division of the middle layer is found here. The grooves of the sensory lines reach thus down near to or even into the basal layer of the exoskeleton.

Turning now to the true Cephalaspids, we can first note that the grooves of the sensory lines occur both in species with continuous and discontinuous superficial layer, and that in the latter case they are situated in such places where the superficial layer is absent (e. g. *C. signata,* pl. 114:1; *C? pedata,* pl. 68:1).

We find, as far as observed, that in the Cephalaspids the sensory lines form comparatively shallow, open grooves, which reach down

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[1] A similar view is also held by Bölau (1951).

into the outer division of the middle layer of the exoskeleton, and that the mucous canals are in communication with these canals (distinctly seen in *Hoelaspis,* pl. 77:1, but also e. g. in *C. signata,* pl. 114:1; cf. Denison 1951b, fig. 37).

When the exoskeleton is subdivided into polygonal areas by means of circum-areal mucous canals or grooves, the grooves of the sensory lines are not situated in these mucous grooves but traverse the polygonal areas in their middle, as observed in *C. aarhusi, C. broughi, C. signata* (pls. 28:1; 114:1) and others (cf. Stensiö 1932, pls. 23:1; 24; 31; 42). In *C? pedata,* however, the grooves of the sensory lines lie in the intertubercular spaces, in the broad grooves, which are thought to be grooves of the mucous canal system, and here the sensory line grooves are provided with lateral walls of their own, which separate them from the mucous grooves, in which they are lodged (pl. 68:1). In *"Procephalaspis" oeselensis* the sensory line canals are said to be circum-areal canals (Denison 1951b, p. 211) but this is not evident from the published figure (Denison 1951b, fig. 37A).

Thus the sensory line grooves of the Cephalaspids have in their disposition no relation to the circum-areal canals or grooves of the mucous system, and are in communication mainly with the intra-areal canals (or grooves), when the mucous canal system is so differentiated.

From what is seen of the development of the sensory lines in the Cephalaspids we must assume that the grooves of the sensory lines and the mucous canal system represent two different structures or organs with different function. The relation between them is only topographical, but, if we assume that the mucous canals have lodged a slimeproducing organ (cf. Stensiö 1927, p. 39; 1932, p. 74; cf. also Matveyev 1945, p. 532—533) and this seems to be a rather probable interpretation, the communication between the mucous canals and the sensory line grooves must appear quite natural, if we remember the analogous fact that the sensory line canals in fishes are filled with slime, produced by mucus cells in the wall of these canals (cf. Cole 1899, p. 192).

From the above survey we find, that the sensory lines in the living Osteostraci were not situated in the epidermis but sunk as grooves or canals into the corium, and we find furthermore that the sensory lines lay much deeper in the corium in geologically old members of the Osteostraci, than in the Cephalaspids proper, and finally that at least in *Dartmuthia* and in *Tremataspis* the sensory lines were situated in closed canals or almost completely covered grooves but that in the Cephalaspids proper the sensory lines formed open grooves in the exoskeleton.

Finally we may in this chapter consider a case of secondary growth in the exoskeleton. In fig. 8 a section of the exoskeleton of *Tegaspis kolleri* is represented, and we find here some conditions, which must be interpreted as appositional growth of a tubercle. The primary

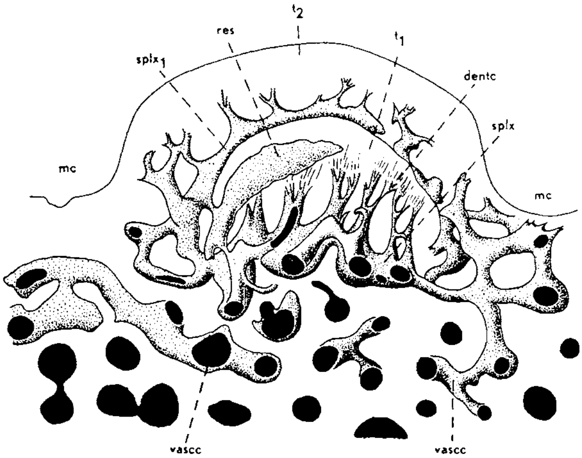

Fig. 8. — Composite tubercle in the exoskeleton near the lateral margin of the cephalic shield of *Tegaspis kolleri,* showing resorption phenomenon and appositional growth. × 100.

dentc, dentine-canals; *mc,* mucous grooves; *res,* cavity, formed by resorption; *splx,* primary subepidermal vascular plexus; *splx*$_1$, secondary subepidermal vascular plexus; *t*$_1$, primary tubercle; *t*$_2$, secondary tubercle; *vascc,* horizontal vascular canals, possibly disposed as radiating canals.

tubercle *(t*$_1$*)* with canals of the subepidermal vascular plexus *(splx)* and dentine-canals *(dentc)* arising from them contains in a part of its upper half a large cavity *(res),* very probably caused by resorption. Above the dentine-layer of this tubercle *(t*$_1$*)* there is a layer with vascular canals, an additional subepidermal vascular plexus *(splx*$_1$*),* which is connected with the primary subepidermal plexus and with the underlying horizontal vascular canals *(vascc),* and outside of it is a thick layer of dentine. Thus there is formed a secondary tubercle *(t*$_2$*),* superimposed upon the primary one *(t*$_1$*),* both forming a composite tubercle, which, however, is not to be distinguished from the simple ones in external view.

The conditions here remind much of those in a superficial "blister" in Osteolepids (Jarvik 1950, pp. 24—26; fig. 3) and the development of the secondary tubercle and that of a superficial "blister" are very probably analogous (cf. also Gross 1935, fig. 9; Ørvig 1951, fig. 4A).

Such cases of appositional growth of tubercles (and thus of the exoskeleton in general) are evidently very rare in Cephalaspids. I have only observed them in a specimen of *Tegaspis kolleri* and they are figured in a *Cephalaspis* sp. by Ørvig (1951, fig. 11B; cf. p. 376) but similar structures are also seen in *Cephalaspis salweyi* (Stensiö 1932, pl. 66:1) and possibly in *Hemicyclaspis (?) lightbodii* (Stensiö 1932, pl. 63:3). They have no real significance for the question as to the general growth of the exoskeleton, about which we know very little indeed (cf. Denison 1947, pp. 362—365).

We can finally note that the structure of the exoskeleton in the

Spitsbergen Cephalaspids and in the Osteostraci in general is subject to great variations, but we can not find that the exoskeleton in geologically older forms is in general better and more completely developed than in younger forms, and there is thus no indication that the exoskeleton in the Osteostraci was on the whole in a regressive state of development (cf. Stensiö 1932, p. 27; Denison 1951a, pp. 170—173; 1951b, p. 217).

The endoskeleton.

As well known, the endoskeletal component of the cephalic shield, the presence of which in the Osteostraci was first established by Stensiö (1927), is a very complex structure.

The endoskeleton is completely ossified in all species of *Boreaspis* (as pointed out for *B. rostrata* by Stensiö 1927); in all other forms of the Spitsbergen Cephalaspids it probably consisted of cartilage or a cartilaginous tissue, provided with a perichondrial bone-layer.

These endoskeletal bone-layers are, however, not always present in the actual fossils or, when present, not developed to the same degree in different specimens (cf. Stensiö 1927, pp. 31—32; 1932, pp. 10—13). The divergences in this respect probably are caused by different factors or a concurrence of several different factors. A secondary cause of the absence or the bad preservation of the endoskeleton can be unfavourable conditions during the decomposition of the animal or during or after the fossilization, including a possible selective dissolution of the chemical components in the bone-tissues; and this is probably the specific cause in very many instances. A primary cause can be a feebler development or a non-development of the bone-layers in question and this, in its turn, can be due to a constitutional factor in the species, which prevents the development of the bone-layers or only allows a moderate ossification of the endoskeleton, or it can be due to the fact that the ossification had not yet begun or was not completed when the animal died and became embedded in the sediment.

Very little is known of the progressive ossification of the endoskeleton during the life of the individual animal. It has been made probable that the skeleton of the Osteostraci became ossified only with maturity (see above, p. 47), and this has been substantiated by the observations of Denison (1947, pp. 358—365) on the growth of the exoskeleton in *Tremataspis*. He has also shown that the ossification of the exoskeleton proceeded in centripetal direction. As Denison's research concerned only the structure of the exoskeleton, he gives no specific informations as to the development of the endoskeleton.

Some observations on *Tremataspis* have made it conceivable that

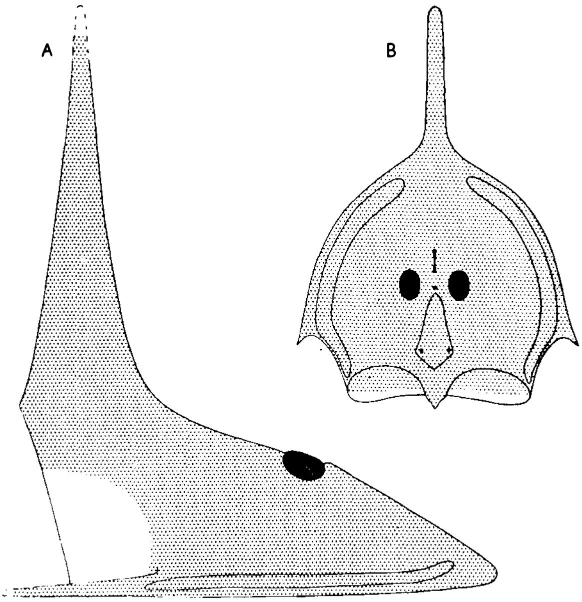

Fig. 9. — Cephalic shields, A, of *Cephalaspis hastata,* in lateral view, B, of *Boreaspis robusta,* in dorsal view. Endoskeletal component of the shield marked by shading. A, nat. size; B, × 2.

the ossification of the endoskeleton and of the exoskeleton took place in the same way and, thus, proceeded from the periphery and inwards. It has namely been found that in *Tremataspis* the bone-layers became more and more delicate in centripetal direction, and finally disappeared, while the peripheral parts of the endoskeleton, near the exoskeleton, were rather strongly ossified. We also find in different specimens of *Tremataspis,* which are found together, and which most likely have been exposed to similar conditions after death, various stages in the state of preservation of the endoskeleton, from specimens with a rather well preserved endoskeleton to such in which it is absent. In how far these conditions were prevalent in the Osteostraci can not yet be told but they seem possibly to be of some significance.

We cannot say in a general way whether the absence or the poor development of the endoskeleton in a fossil Cephalaspid is caused by this factor or another, and it is, with regard to the Spitsbergen Cephalaspids, impossible definitely to say whether "the Cephalaspids in general during the time from the Upper Silurian to the lower Devonian underwent regressive development with regard to the degree of ossification of the endoskeleton" (Stensiö 1932, pp. 12—13; see also 1927, pp. 31—32) or not.

After the foregoing discussion it seems to be of no general interest to give a survey of the state of preservation of the endoskeleton in different species, and the reader is in this respect referred to what is said in the decription of each species.

The endoskeleton constitutes a major part of the cephalic shield, and underlies the exoskeleton in all places, where this is developed, with the exception of certain, most often posterior and postero-lateral, portions of the inter-zonal part. The extent backwards of the endoskeleton is thus in the main as shown by Stensiö (1927, figs. 7, 8; 1932, figs. 3, 4). The Spitsbergen *Cephalaspis* species (figs. 62, 66—67), *Ectinaspis* (fig. 76), *Tegaspis* and *Nectaspis* (figs. 104, 105B) agree in most cases with the *Cephalaspis* species figured by Stensiö (1927, fig. 7; 1932, fig. 3) and the genera *Axinaspis* and *Acrotomaspis* are in this respect similar to *Kiaeraspis* (cf. Stensiö 1927, fig. 8; this paper, pl. 100:1).

In *Benneviaspis, Hoelaspis* and *Boreaspis* the endoskeleton in the inter-zonal part dorsally extends backwards as far as or almost as far as the exoskeleton, and ventrally ends only slightly ahead of the posterior end of the exoskeleton (fig. 9B). We can furthermore note that the interior of the rostral process in *Hoelaspis* and *Boreaspis* is filled up with endoskeleton (fig. 9B; cf. Stensiö 1927, p. 145).

In many *Cephalaspis* species the endoskeleton dorsally extends very far backwards, on to the posterior angle of the inter-zonal part, and, when a dorsal spine is developed, partly or completely fills up the interior of this spine (fig. 9A; pls. 35:1; 56:3).

According to Stensiö (1927, p. 29) the endoskeletal component of the cephalic shield comprises the whole endocranium, a dorsal part of the visceral endoskeleton, the endoskeletal shoulder-girdle and, finally, a pronephros component.

We shall now briefly consider the nature of the hindmost part of the "endocranium". The occipital region was thought by Stensiö (1927, p. 48) to include the whole part of the endoskeleton lying behind the otic region of the endocranium. It was thought that the neural ridge, present on the ventral face of the occipital region, was in the living forms continued backwards by certain cartilaginous parts behind the "foramen magnum", as preserved in the fossil state. It was also assumed, that there must have been a gradual transition between the neural ridge and the vertebral column. On this assumption it is impossible to draw a distinct boundary between the endocranium and the postcranial axial endoskeleton. The occipital region is considered to be short in species with a short inter-zonal part of the shield and long in those with a long inter-zonal part, and it would thus be extremely long in such a form as *Kiaeraspis.* If we furthermore regard a *Dartmuthia,* in which the dorsal endoskeleton reaches as a long chord on to the posterior end of the cephalic shield (cf. Wängsjö 1944, fig. 1), it appears unreasonable to include the whole of this endoskeletal structure in the endocranium. In some *Cephalaspis* species the cephalic shield is provided with a well developed dorsal spine which, as said above, is composed not only of exoskeleton but also includes an endoskeletal component, and as this spine most probably is a transformed anterior part of the dorsal median fin-fold (Kiær 1911, p. 16; Stensiö 1927, p. 26; 1932, pp. 68—69), its endoskeleton certainly must have been derived from quite another primordium (cf. Schaffer 1901; Schmalhausen 1912; 1913) than the real occipital region which always is developed from transformed neural arches. The endoskeleton of the dorsal spine cannot be included with the occipital region solely on the basis that it is a median endoskeletal structure, continuous with the endocranium and lying postero-dorsally to it, without paying regard to its possibly different developmental history. We must stress the fact that the endoskeleton of the dorsal spine lies dorsally to the neural canal and that it most probably is not a part of the axial skeleton. It is also pointed out by Stensiö (1927, p. 50) that the hindmost part of the "occipital region" in a *Cephalaspis* sp. (without any dorsal spine) has no relations to the neural canal but projects backwards as a process above the vertebral column. This is the case also in *Kiaeraspis* but in this form the process is much longer than in the *Cephalaspis* sp., just mentioned. In *Dartmuthia* the long posterior skeletal chord, referred to above, has no relations to the neural canal. It lies dorsal to it, is epiaxial and does not belong to the axial skeleton.

Another interesting feature in *Dartmuthia* is the long backward extension of the endoskeleton as a strand on the lateral sides of the cephalic shield.

We find that in the posterior part of the cephalic shield in *Dartmuthia* the endoskeleton is formed in those places, where the median and lateral fin-folds or rudiments of them are supposed to be or have been developed, and it seems thus very probable that the dorsal and lateral endoskeletal strands, mentioned above, really represent ossifications in a longitudinal plate of skeletogenous tissue, lying in the median dorsal and the lateral fin-folds (cf. the ontogeny of the median or paired fins in Petromyzonts and in fishes, Balfour 1881; Schaffer 1901; Braus 1904; Schmalhausen 1912; etc.).

These endoskeletal structures which, probably both, are present also in other Cephalaspids (and the dorsal one of them is here partly represented by the endoskeleton in the dorsal spine), will be referred to as the dorsal and the lateral inter-zonal endoskeleton, and it will be emphasized that they constitute postcranial divisions of the endoskeleton of the cephalic shield.

Anteriorly the lateral inter-zonal endoskeleton is probably continuous with and passes into the zonal endoskeleton (the shoulder-girdle) without any boundary, and it must originally have been part of the same initial structure as this division, since the zonal endoskeleton is to be regarded as the transformed anterior part of the deep tissues in the lateral fin-fold (cf. the development of the paired fins and their girdles in fishes, e. g. Goodrich 1930, pp. 123—144, 163—164, 169). The boundary between the lateral inter-zonal and the zonal endoskeleton must be difficult to determine if and when they both are fully developed. In *Dartmuthia* the presence or development, if present, of the zonal endoskeleton is still unknown. In the Spitsbergen Cephalaspids all the endoskeletal structures lying in the lateral sides of the inter-zonal part and behind undoubtedly zonal endoskeleton are, for the sake of convenience, regarded as belonging to this division.

Most anteriorly in the inter-zonal part of the shield the dorsal inter-zonal endoskeleton came into contact, during ontogeny, with the skeletogenous tissues around the spinal cord, and in the fossils it is impossible to determine the boundary between the dorsal inter-zonal endoskeleton (epiaxial) and the axial skeleton; the inter-zonal endoskeleton is also wholly continuous with the endocranium and no distinct boundary can be drawn between them.

With regard to the peculiar development of the endoskeleton as a single continuous mass in the shield of the Osteostraci, the question as to the limit between the head and the trunk or, more explicitly, between the endocranium and the postcranial endoskeleton, which in all vertebrates is a very difficult one, is here still more intricate, and, since we shall never know the ontogenetical development of the endoskeleton in these forms, it cannot be answered adequately and definitely (cf. Koltzoff 1902, p. 573; Johnston 1905b, pp. 229—230).

In the fossils the boundary between the two regions must be drawn quite arbitrarily, and, since there is no possibility to fix it at any point in the most posterior part of the endoskeleton (as hinted to above), it will here be drawn in the region of the neural tube and the notochord, at some place behind the exit of the vagus canal from the cavum cerebrale and before the exits of the canals for the first spinal nerve from the neural canal. It will thus be set down between the posterior uniformly narrow neural canal, which has enclosed the medulla spinalis, and the widened part of the cavum cerebrale, lying in front, which enclosed the medulla oblongata. The dorsal part of the occipital region will be considered to extend somewhat farther backwards than the ventral part, or as far as to enclose the openings of the ductus endolymphatici. Posteriorly the occipital region is continuous, dorsally with the dorsal inter-zonal endoskeleton, and ventrally and medially with the postcranial axial endoskeleton, "the vertebral column".

With this delimitation of the occipital region, and thus of the posterior boundary of the endocranium, we must distinguish yet another division in the endoskeleton, viz. that enclosing (wholly or partly) the neural canal and, partly, the notochord, and which thus consists of ossifications in the perichordal skeletogenous tissues. This division is here called the inter-zonal axial endoskeleton (or the postcranial axial endoskeleton). It forms the posterior and major part of the neural ridge and the roof of the neural canal and, behind the ridge, the roof of the neural groove; it has free ventral, postero-ventral and, partly, lateral sides and is continuous anteriorly with the occipital region of the endocranium and dorsally with the dorsal inter-zonal endoskeleton.

It must be noted that in the fossils the dorsal and the axial inter-zonal endoskeleton have no fixed posterior limit, the extent backwards of the regions being dependent of the length of the inter-zonal part. They are in general well developed and long in species with a long inter-zonal part and short in those with a short inter-zonal part. In the living forms both the dorsal inter-zonal and the postcranial axial endoskeleton extended far backwards in the trunk but were here represented by unossified connective tissues.

The demarcation in the endoskeleton between the endocranial and the postcranial (dorsal and axial) inter-zonal endoskeletal divisions reflects the subdivision of the cephalic shield into the cephalic division proper and the trunk division (Stensiö 1927, p. 20).

More or less complete remains of all the divisions, distinguished in the endoskeleton of the Spitsbergen Cephalaspids and mentioned above, have been observed in the material treated in this paper.

The endocranium.

The endocranial division of the endoskeleton can only arbitrarily be identified and distinguished from the rest of the endoskeleton, as it is continuous with and merges imperceptively into the dorsal parts of the visceral endoskeleton and the inter-zonal endoskeleton.

The endocranium encloses the brain-cavity and the ethmoidal cavity, as well as the labyrinth cavity and the orbits, in addition the proximal parts of the canals outgoing from these cavities (and some canals wholly lying within the endocranium).

The roof of the oralo-branchial chamber is regarded as being mainly of visceral origin and will be dealt with in connection with the visceral endoskeleton.

In the endocranium ethmoidal, orbito-temporal, otic and occipital regions have been distinguished (Stensiö 1927, p. 48), and as for their delimitations and extents in the endocranium the reader may consult the papers of Stensiö (1927) or Holmgren & Stensiö (1936; cf. however, what is said in the present paper about the occipital region).

In the subsequent account it will often be unpractical to keep within the limits of a region when describing certain canals or other structures, and in such cases I shall without interruption and in one place describe such structures which are in a certain way connected with each other, even if they belong to different regions.

The ethmoidal region encloses the ethmoidal cavity in which three divisions have been distinguished (Stensiö 1927, pp. 124—125; Holmgren & Stensiö 1936, p. 252), viz. a dorso-posterior tube-shaped division for the olfactory organ, an antero-ventral likewise tubeshaped division for the anterior part of the hypophyseal pouch, and a middle narrow division between these two sections. In general these three divisions of the ethmoidal cavity communicate with the exterior through the respective divisions of the naso-hypophyseal opening.

In *Nectaspis,* which has an anterior opening for the hypophyseal duct and a posterior nasal opening proper through the exoskeleton, there is a middle slit-like opening in the endoskeleton (pls. 110:1; 111:3-4) covered by the exoskeleton and thus the middle division of the ethmoidal cavity opens on the dorsal face of the endoskeleton but is closed to the exterior.

In *Cephalaspis excellens* the middle division of the ethmoidal cavity is closed dorsally by a part of the internal bone-layer, and there is formed a saddle-like depression in the roof of the ethmoidal cavity between an anterior and a posterior opening into the outer face of the endoskeleton (pls. 13, na_1, na_2; 15:2), or, expressed in other words, from the closed ethmoidal cavity issue in antero-dorsal direction two short separate canals, an anterior one for the outer part of the hypophyseal pouch and a posterior one for the nasal tube.

It is worthy of note that in all Cephalaspids, sufficiently known, even in those forms with a common naso-hypophyseal opening, the hypophyseal sac and the nasal tube must have opened to the exterior by separate openings, and that in the Cephalaspids there was not formed a common naso-hypophyseal tube as in the modern Cyclostomes (cf. e. g. Bütschli 1921, figs. 503—504).

As described by Stensiö (1927, p. 125) the postero-dorsal division of the ethmoidal cavity is tube-shaped, and it seems thus probable that this division only lodged the nasal tube, which led to the olfactory organ, and that the olfactory organ itself was situated slightly postero-ventral to this division, in the most antero-dorsal part of the so-called cavum cerebrale cranii, which is distinctly and often considerably wider than the "ethmoidal cavity" (Stensiö 1927, figs. 15, 20, 22—23, 27; pls. 13:3; 47:1, *tel;* this paper, pls. 90:5; 93:2). This assumption is also to a certain extent based upon what is known of the olfactory organ and its development (Retzius 1893, pl. 24:1-3; Lubosch 1905;

Imamura 1928; Matthes 1934; etc.) and the configuration of the olfactory bulbs of the telencephalon in recent Cyclostomes (Müller 1839, pls. 2:8-9, 11-12; 3:3-5; Wiedersheim 1880, pl. 1:3-6; Ahlborn 1883, pl. 13; Retzius 1893, pl. 24:1-4, 6; Johnston 1902a; 1912, figs. 3—4; Worthington 1906, pl. 8:1-3; Sterzi 1907, figs. 18—21, 70, 160, 165; Bütschli 1912, fig. 404; Herrick & Obenchain 1913, figs. 1—2; Saito 1930, pls. 7—10; Jansen 1930, figs. 1—3; Larsell 1947, figs. 1, 7; Heier 1948, figs. 1—2; etc.; cf. also Goodrich 1909, figs. 21, 25; Matthes 1934, fig. 663; Parker & Haswell 1940, fig. 109). It is thus probable that the olfactory organ in the Cephalaspids was not lodged in such a narrow and high cavity as indicated in the restorations by Stensiö (1927, fig. 32) and that it did not occupy any part of the middle division of the ethmoidal cavity (cf. Stensiö 1927, p. 125). The median ridge observed by Stensiö in the roof of the cranial cavity between the pineal opening and the posterior division of the naso-hypophyseal opening in a *Cephalaspis* specimen (Stensiö 1927, p. 141; figs. 15, 23; pl. 80) can possibly indicate that the olfactory organ in the Cephalaspids was bipartite, divided by a simple median septum, as it is in the *Petromyzon*-larva (Peter 1901; Lubosch 1905; Imamura 1928). If the assumption as to the position of the olfactory organ put forward above is justified then the foremost part of the cavum cerebrale as defined by Stensiö (1927, pp. 135—142) is really a part of the ethmoidal cavity.

At the transition between the ethmoidal and the orbito-temporal regions the floor of the endocranium is pierced by the paired carotid canal (pls. 4:2; 8:2; 14; 15:1, 3-4; 16; 17; 69; 83:1-2; 86:2; 112:1, *acar)* in the usual manner (Stensiö 1927, pp. 111—112).

In a specimen of *Boreaspis macrorhynchus,* however, the two carotid canals issue from the aorta groove in about the median line, one canal lying before the other (pl. 93:1, *acar).* The posterior canal runs in dorso-lateral, the anterior one in postero-dorso-lateral direction, and they both open into the cranial cavity in the normal way and thus at about the same transverse level (pl. 94:2, *acar).* These conditions furnish additional proof of the hypothesis that the aorta (in this place) really was unpaired (cf. Stensiö 1927, p. 174).

As usual in the Cephalaspids (Stensiö 1927, p. 112) a groove leads from the inner opening of the carotid canal in the lateral wall of the ethmoidal cavity to the opening of the canal for the a. facialis (pls. 3:2; 4:1; 8:2; 14; 15:1; 17; 86:2; 109, *afac).* An independent canal for the a. facialis wholly outside of the ethmoidal cavity, as in *Kiaeraspis* (Stensiö 1927, p. 112; figs. 21—22), has not been observed in any of the specimens so far examined.

In a specimen of *C. excellens* (pl. 15:3-4) we find, however, some aberrant conditions with regard to the canal of the a. facialis. In pl. 15:3 a pair of canals *(afac)* is seen to pierce the floor of the division of the ethmoidal cavity for the hypophyseal sac at some distance in front of the inner openings of the carotid canals *(acar);* the canal *afac* on the right side issues somewhat ahead of the corresponding canal on the left side. In the continuation of each canal there is a groove running in postero-dorso-lateral direction in the wall of the cavity. These grooves pass into a pair of canals, issuing from the lateral side of the ethmoidal cavity; the canals are in pl. 15:4 seen to split into two branches. The canals *afac* in pl. 15:3, although lying anteriorly to the carotid canals and issuing independently of them from the aorta groove, evidently correspond to the canals for the a. facialis in other Cephalaspids; the a. facialis in this specimen had thus arisen directly from the aorta and not as a branch of the a. carotis.

In a specimen of *C. exilis* (pl. 27:1) a canal is seen issuing from the antero-dorso-lateral side of the canal for the left a. carotis *(acar),* and this canal is most probably the canal for the a. facialis.

During its antero-dorso-lateral course to the upper face of the ethmoidal region the canal of the a. facialis divides into some branches, of which the antero-dorsally directed canal *afac* must be considered as its anterior continuation. Distally, after having reached the outer face of the endocranium, it continues in antero-ventral direction over to the visceral endoskeleton. The lateral canal *aad* is the most conspicuous branch of the main canal (pls. 3:2; 4:2; 8; 10; 13; 15:2; 23:1; 34:1; 36:1; 38:2; 62:1; 106, *afac, aad).* In some specimens also a posteriorly directed branch *(afp)* has been observed (pls. 13; 15:2; 19:2; 36:1; 38:2; 106; 107).

The canal *afac* branches frequently (pls. 8:2; 10; 23:1; 62:1) and, as these branches intersect in some places (pl. 10:1, *afac,* V_1*?)* it seems very probable that some of them enclosed structures other than arteries, and since these canals often run in a fairly straight direction, they most probably gave passage to nerve-fibres. In *Cephalaspis hoeli* the branches in question are distributed to the dorso-median part of the cephalic shield immediately antero-laterally to the anterior division of the naso-hypophyseal opening (pl. 101, V_1*?).* By comparison with modern Cyclostomes (cf. Fürbringer 1875; Allis 1903a; Johnston 1905a; Worthington 1906; Tretjakoff 1927a; Cords 1929; Lindström 1949) we must conclude that these nerve-fibres were general cutaneous fibres belonging to the n. profundus (ophthalmicus; V_1).

In *Nectaspis areolata* we find in the holotype a small canal (pls. 106; 107, V_1*?)* issuing from the canal for the a. facialis immediately after it has reached the dorsal face of the endocranium and running for a short distance in antero-lateral direction just in front of the orbit; this canal has the appearance of a nerve-canal and has possibly given passage to a branch of the n. profundus.

In the same specimen of *Nectaspis areolata* there is a distinct canal (pls. 108; 109, *afm),* which issues from the canal of the a. facialis *(afac)* just after its exit from the ethmoidal cavity, and which runs in antero-dorso-medial direction to the outer face of the endocranium between the opening for the hypophyseal duct and the nasal opening proper. It enclosed a median branch of the a. facialis or possibly a branch of the n. profundus.

In the same specimen there is seen a small canal (pl. 109, *n),* coming from the antero-median part of the orbit or from the transitional part between the cavum cerebrale and the orbit (thus from the roof of the canalis opticus) and running in dorso-median direction to the lateral part of the dorsal side of the interorbital wall postero-laterally to the nasal opening proper (pl. 108, na_2) and laterally to the pineal opening (pl. 108, *pin).* As this region of the shield was drained by a vein in the canal *vso* (pl. 107), the canal *n* very probably did not transmit a vein, and, as its origin lies rather laterally, it is not very conceivable that it lodged an artery from the internal carotid; most probably the canal gave passage to a dorsal branch of the n. profundus or the r. ophthalmicus superficialis lateralis.

In the holotype of *C. excellens* we find some canals or canal fragments of fine calibre on the dorsal face of the ethmoidal region in the circum-nasal fossa (pls. 13; 15:2). A canal *(vso),* which in another specimen (no. A30064, not figured) is seen to issue from the dorso-median part of the orbit, runs in antero-median direction from a point, medially to the anterior part of the orbital opening. It gives off branches in anterior and posterior direction and leads into the short canal for the nasal duct near its opening; this canal *(vso)* must correspond to the canal $v.\ so_1$ for the anterior supraorbital vein, described in *Kiaeraspis* and *C. verruculosa (*Stensiö 1927, p. 134; figs. 27, 49; pl. 39). Below this canal and thus slightly under the dorsal face of the endocranium are seen some horizontal canal fragments, which evidently all belong to one and the same canal *(su).* It is much narrower than the canal *vso,* and runs forwards in bending slightly medially; as it passes ventrally to small openings into the dorsal side of the endocranium, it very probably sends small branches upwards to these openings. As the course of the canal *su* rather closely corresponds to that of the groove in the exoskeleton for the supposed supraorbital sensory line *(soc),* it conceivably enclosed nerve-fibres belonging to the r. ophthalmicus superficialis lateralis and supplying neuromasts in this line.

The lateral branch *(aad)* of the canal for the a. facialis (corresponding to the main canal for the a. facialis in the terminology of Stensiö) first runs as usual in a lateral direction and then gradually curves into a posterior direction, following rather closely the anterior and lateral borders of the orbital opening; it generally ends near the postero-lateral corner of this opening. On account of its position near the orbit, it will here be called the canal for the a. adorbitalis (the adorbital artery); it is seen in several specimens (pls. 8:1; 10; 19:2; 23:1; 24:2; 36:2; 62:1; 93:2; 98:1). It gives off, as is well known, several antero-lateral branches, which will be further considered in the chapter on the visceral endoskeleton.

It can also be noted that the lateral parts of the ethmoidal region are traversed by a canal for the preorbital division of the v. capitis lateralis, and laterally to this canal by the canal for the r. maxillaris trigemini (n. profundus, Stensiö), and most laterally by the first nerve canal for the lateral sensory field, as is known from the descriptions by Stensiö (1927, 1932).

In a specimen of *C. excellens* a canal (pl. 15:4, vls_2) is seen to enter the orbit just laterally to the exit of the canal for the r. maxillaris trigemini (V_2). This is the canal for the second dorso-lateral superficial vein, which in this specimen, most unusually, enters the orbit directly and not by means of the canal for the preorbital division of the v. capitis lateralis (cf. Stensiö 1927, pp. 188, 223).

We can finally add that some fine canals, having evidently carried somatic-sensory nerve-fibres, of the general cutaneous and in some cases certainly of the lateralis system, issue from the antero-lateral part of the orbit, running in antero-lateral direction to the superficial parts of the visceral endoskeleton (pls. 12:5; 15:3-4; 36:1; 38:2, *n, bu);* in some cases they are seen to open into vascular canals (pl. 15:4, *n*, vls_2).

Turning now to the orbito-temporal region of the endocranium, I have nothing to add to the descriptions by Stensiö (1927, pp. 94—100; 1932, pp. 32—33; Holmgren & Stensiö 1936, pp. 253—254) with regard to its general structure and its relation to other parts of the endoskeleton, but will immediately go on to a consideration of its canals.

It will first be noted that in some species at the place of the foramen opticum is formed a very short canal connecting the cavum cerebrale cranii with the orbit (cf. Stensiö 1927, figs. 15, 21). Thus we must speak of a canalis opticus instead of a fenestra optica.

As mentioned just before, the lateral part of the ethmoidal region is traversed by the canal V_2, here called the canal for the r. maxillaris trigemini (see below; corresponding to the canal "V_1" of Stensiö), which opens into the antero-ventral part of the orbit (cf. Stensiö 1927, pp. 113, 125). And we can now observe that a posterior continuation of this canal is found in the shape of a more or less distinctly marked groove in the floor of the orbit beginning at the opening of the canal (pls. 3:2; 4:1; 8:2; 14; 15:1, 3-4; 16:1; 17; 39:1; 40:3; 81:1; 83:1;

86:2). In some specimens of *C. oreas, C. excellens, C. doryphorus, Boreaspis robusta* and *B. puella* (pls. 8:2; 16:1; 39:1; 81:1; 83:1) this groove can be followed in postero-median direction to the postero-ventro-median corner of the orbit near to or on to the opening of the trigeminus-lateralis chamber (see below, p. 67).

This is a very important fact as it shows that the nerve transmitted in the canal V_2, if we follow it in centripetal direction, must, after entering the orbit, have run in this groove in the floor of the orbit all the way on to its ganglion in the trigeminus-lateralis chamber or, if a groove is not or only partly developed, have in any case been situated closely to the floor of the orbit. The nerve must thus have had such a position that it crossed the n. opticus, passing ventral to it or that it in any case lay morphologically ventrally to the n. opticus. Consequently it can not have been a n. profundus as maintained by Stensiö since in all vertebrates, without exception, the n. profundus has its path dorsally to the n. opticus.

On comparison with modern Cyclostomes (cf. Fürbringer 1875, pp. 32, 61, 63; fig. 23; Johnston 1905a, pl. 5; Worthington 1906, p. 166; fig. 14; Tretjakoff 1927a, pp. 387—389; figs. 10—11; Cords 1929, pp. 223—225; figs. 1, 3—4; Lindström 1949, figs. 9, 24, 29) and fishes (cf. Allis 1897, pp. 603, 605, 607; figs. 20—21, 25, 30; 1903b, p. 254; fig. 55; 1922, pp. 275—276; figs. 45, 49; Herrick 1899, pp. 332—348; pl. 15; 1900, pp. 279—282; 1901, pp. 196—201; Norris 1925, pls. 1—2, 4—6; Norris & Hughes 1920, p. 336; figs. 15—17, 35, 51; Pankratz 1930, fig. 10; Pope 1938, pp. 418—419; etc.) we find that certain parts of the n. trigeminus (often associated with the n. lateralis anterior) have a similar course as the nerve in the canal (and groove) V_2, and that this nerve with regard to its course within the orbit can be compared most closely with the r. maxillaris of the n. trigeminus (n. subopticus) in *Petromyzon*. It can be noted that Allis (1931a, pp. 525—526) regards the "n. profundus" in the Cephalaspids (i. a. under the assumption that it ran ventrally to the n. opticus instead of dorsally to it) as homologous to the r. maxillaris V in *Petromyzon,* and that Holmgren & Stensiö (1936, pp. 265, 279) with regard to the course of the "n. profundus" in the visceral endoskeleton, express a surmise that this nerve in the Cephalaspids corresponded partly with the n. maxillaris in the Petromyzonts (cf. Lindström 1949, pp. 445—446).

In this paper the nerve will be regarded as to some degree homologous to the r. maxillaris trigemini in the Cyclostomes, and will be called the r. maxillaris trigemini, and its canal the canal for the r. maxillaris trigemini *(V_2).*

In the antero-ventro-lateral part of the orbit, postero-laterally to the opening of the canal V_2, just considered, there is another opening for a nerve canal V_3 (corresponding to the canal "V_2" in Stensiö's descriptions). The proximal course of this canal and its opening into the orbit are seen in several specimens (pls. 3:2; 4:1; 8:2; 16; 17; 86:2, V_3, V_{3a}).

In *C. oreas* (pl. 8:2) a faintly marked groove in the floor of the orbit starts from this opening and runs in postero-lateral direction, and in *C. doryphorus* (pl. 39:1) and some specimens of *C. excellens* (pl. 16:1; cf. pl. 15:3) we find a well marked and distinct groove (in *C. excellens* in places covered with a thin bone-lining and thus forming a partly closed canal) in the floor of the orbit all the way from the opening, just referred to, and leading to an opening in the postero-ventral part of the orbit for a canal to the brain-cavity (corresponding to the canal "*l*" in Stensiö's descriptions).

In *Boreaspis robusta* (pl. 81:1) the canal V_3 enters the orbit in its lateral part and is continued in postero-median direction by a well marked groove in the postero-ventral wall of the orbit. A corresponding groove is seen also in a specimen of *B. puella* (pl. 81:3, V_3) and in the holotype of *Nectaspis areolata,* in which latter specimen the groove is very deep and forms a partly closed canal.

In another specimen of *N. areolata* however, the canal V_3 runs entirely outside of the orbit, along its postero-lateral side. In its further course, between the labyrinth cavity and the trigeminus-lateralis chamber, it runs in postero-median direction to the brain-cavity or, more exactly, towards the transition between the labyrinth cavity and the cavum cerebrale, i. e. towards the short canalis acusticus (fig. 12; pl. 112:1).

The canal V_{3p} (corresponding to the proximal part of the canal V_3 in the specimen of *N. areolata,* just mentioned, and to the canal "*l*" in the Cephalaspids described by Stensiö) enters the brain cavity as usual by means of the canalis acusticus (pls. 14; 15:1; 16:1; 17; 39:1, *cacu)* but in *C. acuminata* (pl. 3:2) it evidently runs directly to this cavity in front of the canalis acusticus. In *C. excellens* the canal is continued in postero-median direction by a groove *(*V_{3p}, pl. 17) in the antero-median wall of the labyrinth cavity and this groove could be traced proximally over into the canalis acusticus, where it ends just near the point of communication between this latter canal and the canal *Vm* (see further p. 69).

The canal V_{3p} *("l")* was considered by Stensiö (1927, pp. 86—87, cf. Holmgren & Stensiö 1936, p. 255) to have contained lateralis fibres and to correspond to a nerve which in *Petromyzon* "passes from the otic capsule to the orbit and which consists of the lateralis fibres which accompany the trigeminus branch". Stensiö (1927, p. 103) assumes that the conditions with regard to this nerve in the Cephalaspids were almost exactly as in *Petromyzon,* that its fibres did not become ganglionic until they reached the orbit, and that its ganglion was situated at the bottom of the orbit (cf. the restoration of the brain and the cranial nerves in a Cephalaspid, Stensiö 1927, fig. 43). The nerve-fibres, referred to in *Petromyzon,* are evidently the roots of the lateralis nerve which pass through the capsula auditiva and form the ganglion hypoticum (Tretjakoff 1927a, p. 402), lying closely up to the antero-ventral part of the said capsule (cf. Ahlborn 1884, pl. 18:5; Alcock 1898, pp. 133—136; pl. 2; Johnston 1905a, pp. 159—160; pl. 5; Tretjakoff 1927a, pp. 402—404; fig. 6; Cords 1929, pp. 230—231; Lindström 1949, pp. 386—388). In rostral direction the ganglion gives off a tiny commissure to the n. trigeminus (and n. profundus) and the main nerve, the n. buccalis (or r. buccalis VII).

If we now return to the conditions in the Cephalaspids, we find some facts which directly speak against such an interpretation.

The canal V_3 *("*V_2*")* was regarded by Stensiö (1927, pp. 113, 198) as having lodged the truncus maxillo-mandibularis or the n. trigeminus proper, and the origin of this nerve, a compound ganglion gasseri, to have been situated chiefly in the postero-ventro-median part of the orbit. The n. trigeminus was said to have been accompanied by lateralis fibres from the supposed lateralis ganglion in the orbit (lying laterally to the g. gasseri), but some independent lateralis fibres were also thought to have been given off in lateral direction from the lateralis nerve during its course through the orbit (see Stensiö 1927, figs. 24, 28, 43).

From the above account it is evident, that the nerve in the canal "V_2" and that in the canal *"l"* must have formed the distal and the proximal parts of one and the same nerve, and we have seen that this nerve in (at least one specimen of) *Nectaspis areolata* passed from near the cranial cavity outwards in a canal of its own. The proximal part of this canal (or the canal *"l")* cannot have given passage to the roots of a lateralis nerve while the distal part of the same canal (or the canal "V_2"*)* contained mainly the maxillo-mandibular trunk (cf. also Stensiö 1927, pls. 49—50). We find furthermore from the conditions in some specimens that there is no point in the canal, here called V_3, nor in the floor of the orbit, which is transformed in such a way that it could have lodged a ganglion of this nerve. As, furthermore, it is highly improbable that a ganglion could have been situated within the brain-cavity, it follows that this nerve could not have contained any sensory fibres (if not secondarily enclosed; see below, p. 67). It must have been a purely motor trunk. And although the nerve in its disposition outside of the brain-cavity was quite independent of the nerves in front and behind, it cannot have constituted a complete cranial nerve (a comparison with the eye-muscle nerves is of course quite excluded in this connection) but only a part of such a nerve.

It is now evident that the nerve in the canal V_3 was not a n. buccalis, nor a maxillo-mandibularis trunk (n. trigeminus proper), and neither a n. facialis (as suggested by Lindström 1949, pp. 446—447).

Looking for comparable conditions in the pro-otic nerve-group in recent Cyclostomes and fishes, we find that the disposition of the nerve in question in the Cephalaspids most closely corresponded to that of the motor trunk of the n. trigeminus in the Myxinids (Allis 1903a, pp. 262—263, 274; Holmgren 1919, fig. 27; 1946, p. 56; Jansen 1930, figs. 1—3; Lindström 1949, pp. 332, 346, 352, 436; figs. 9, 15) which, at least proximally, is quite isolated from the trigeminus ganglion and its branches.

We may thus be justified in regarding the nerve, which passed through the canal (or canals and groove) V_3 as a motor trunk belonging to the n. trigeminus, and it is consequently called in this paper the r. mandibularis trigemini, in analogy with the conditions in recent Cyclostomes, and its canal (or canals and groove) is called the canal (the canals and the groove) for the r. mandibularis trigemini *(*V_3*)*.

In some specimens described by Stensiö (1927, pp. 114—115) there are some very fine canals *(bu)* passing through the lateral wall of the orbit and for the most part leading into the canal "$sel_{1,\,2}$" (= sel_1 in this paper), but in some cases running to the outer face of the endoskeleton antero-laterally to the orbit. They were considered to have carried lateralis fibres from the supposed lateralis ganglion in the postero-lateral part of the orbit, and general cutaneous fibres from the g. gasseri. Similar canals are also described by Zych (1937, pp. 86—89) but the nerves in two anterior canals are by him thought to have been associated with the "n. profundus" and to have formed branches of the "n. ophthalmicus lateralis" (they would, according to him, correspond to the canal bu_1 in Stensiö 1927, pls. 21, 28).

In pls. 36:1, 37, and 38:2 in the present paper there are seen several canals, interpreted as canals for somatic sensory nerves, coming from the superficial parts of the visceral endoskeleton and entering the orbito-temporal region of the endocranium. As noted above, similar canals also traverse the lateral parts of the ethmoidal region.

In *C. excellens* (pl. 16:1) a couple of fine canals *(n)* pass from the groove of the r. mandibularis trigemini *(*V_3*)* in the orbit in antero-lateral direction to the canal sel_1, and in *Nectaspis areolata* (pl. 112:1; cf. fig. 12) some very fine and short canals *(n)* pass from the orbit or from the trigeminus-lateralis chamber to the canal V_3.

In *C. oreas* and *C. excellens* (pls. 8:2; 14; 15:1) the floor of the orbit is traversed by some very fine grooves running from the periphery in median and postero-median direction.

All these grooves and canals, now considered, as well as the similar ones previously mentioned in connection with the ethmoidal region, had evidently lodged fine nerves of the general cutaneous and the lateralis systems, corresponding to those in the canals *bu* in the Cephalaspids described by Stensiö, and in the canals *opht. lat* and *bu* in Zych's description. It is also evident from the disposition of some of them that the nerves in them cannot have had their origin in the nerve in the canal V_3, but must have been associated with the nerve in the canal V_2 or have originated in the trigeminus-lateralis chamber. And from what is said above with regard to the structure of the nerve in the canal V_3 it is impossible that any of these nerve-fibres could have been branches from this nerve.

These conditions now lead us to a consideration as to the nature of the endocranial space, which repeatedly has been referred to as the trigeminus-lateralis chamber.

This chamber is a wide canal or deep fossa opening into the postero-ventro-median part of the orbit and reaching in median or postero-median direction near to the median line, where it ends blindly (in some specimens the canal meets in the median line its fellow of the other side and becomes confluent with it). The chamber is connected with the cavum cerebrale by means of several canals of varying size. Stensiö (1927, pp. 97—98) interpreted it as a (posterior) myodome.

The trigeminus-lateralis chamber is seen more or less distinctly in some specimens among the present material (pls. 8:2; 14; 15:1; 16:1; 17; 31:1; 39:1; 40:3; 57:1-2; 112:1, *gch).* It is by Stensiö (1927, p. 97) said to diminish in diameter medially, but this is not a general character for in some specimens, as seen in pls. 15:1 and 112:1, the opening of the canal or chamber into the orbit is distinctly narrower than its middle part, the whole chamber being more or less sac-like in *C. excellens* (pl. 15:1), but fusiform in *Nectaspis areolata* (fig. 12; pl. 112:1). In a specimen of *C. excellens* the chamber is seen (pl. 17) to be indistinctly subdivided into two parts, a larger antero-lateral one, which opens into the orbit and which posteriorly receives a strong canal, and a smaller postero-median part, which is rather rounded.

As said above, Stensiö regarded this chamber as a myodome for some of the recti muscles, and this only on the assumption that, since the orbit attains a rather considerable size, the eye must have been large and well developed and the recti muscles accordingly strong and large, requiring an enlarged area of attachment.

From the conditions in *Aceraspis, Hirella, Ateleaspis* (Heintz 1939, pp. 18—25, 72, 89) and *Tremataspis* (Patten 1912, figs. 238—239; Robertson 1938a, p. 190; and own observations) we know that the eyeball is large, almost filling up the orbit, and that the outer layers (the scleroid and parts of the corneal layers) of the eyeball are heavily ossified in the named genera. In other Cephalaspids the ossification of the eyeball seems to be less developed. It seems, however, probable that the eyeball in all Cephalaspids retained the same relations to the orbit as in the genera mentioned. To judge from the conditions in these there are no indications whatever that the eye-muscles were large and strong. Heintz (1939, p. 24) is of the opinion that the eyeball in *Aceraspis* (as well as in all Cephalaspids) was only slightly movable. Allis (1931a, pp. 514—515, 527) denies the presence in the Cephalaspids of a myodome comparable to that in the Teleostomes (but points out that the so-called myodome in the Cephalaspids resembles to some degree a part of the trigeminus fossa in *Squalus* and the trigeminus fossa in *Polypterus),* but as pointed out by Stensiö (1927, p. 98), if a myodome was present in the Cephalaspids, it must have arisen independently from that in the Teleostomes, and we can thus not expect to find very similar conditions in these cases. As, however, there is nothing in favour of the presence of a myodome in the Cephalaspids and since the fossa in question in some cases (as in *Nectaspis areolata* and some specimens of *C. excellens)* has definitely not the shape of a myodome, I don't think we are compelled to or need assume that a myodome was developed in the Cephalaspids.

From the shape of the chamber and with regard to the several canals entering it from the cavum cerebrale, the chamber or fossa is considered as having mainly contained some ganglionic masses, and, to judge from the nature of the canals and grooves connected with it, it contained the compound trigeminus ganglion and an anterior lateralis ganglion. The chamber is therefore here called the trigeminus-lateralis chamber. As we shall see below, it was also traversed by certain vessels, and it seems also possible that some small parts of the ganglion-complex were situated outside of the chamber in the adjacent part of the orbit.

As is seen from the pl. 112:1 (cf. fig. 12) the orbit in *Nectaspis areolata* has a shallow postero-median recess between the opening of the trigeminus-lateralis chamber and the canalis opticus; this recess can possibly be interpreted as having formed the attachment for one or some of the recti muscles but, of course, nothing definite can be said in this question.

We shall now with regard mainly to the conditions in *Cephalaspis* (cf. Stensiö 1927, pp. 100—110, 197, 199—202) consider in some detail the canals which, coming from the cavum cerebrale, enter the trigeminus-lateralis chamber.

In the *Cephalaspis* specimen, used by Stensiö for his series A of sections (Stensiö 1927, figs. 15—17, 23—24; pls. 77—79; Holmgren & Stensiö 1936, figs. 214—215, 218; cf. this paper, fig. 10) there are on each side seven canals *("Va—d", "Vx", "Vxa", "v. pt")* of varying calibre, which issue from the cavum cerebrale and are in communication with the trigeminus-lateralis chamber; two of them are, however, very small and do not run directly to this chamber but join the canal lettered *"Vd"*. In the *Cephalaspis* specimen in series B of sections (Stensiö 1927, pls. 86—87) there are six such canals (the canals *"Va"* and *"Vb"* forming a single canal), and in *C. exilis?* (series C, Stensiö 1927, pls. 89—93) the canal *"Va"*, *"Vb"* and *"Vx"* are not differentiated, and thus we find here only four canals.

In the present material we find in *C. excellens* only three or four of the canals in question (pls. 15:1; 17) but there are possibly additional canals which have not been revealed by the preparation. In *C. signata* four canals enter the posterior half of the trigeminus-lateralis chamber (pl. 31:1), and in an unnamed *Cephalaspis* sp. (pl. 57) there are seven or eight canals from the brain-cavity which directly or indirectly run to the trigeminus-lateralis chamber.

The most strongly developed of these canals is the one (lettered *"Vd"* by Stensiö 1927, p. 100), which leaves the floor of the cavum cerebrale at a level with the fenestra (or canalis) acustica and enters the posterior part of the trigeminus-lateralis chamber (pls. 8:2; 14; 15:1; 16—17; 31:1; 39:1; 40:3; 57, *Vm*). Its general disposition is as described by Stensiö (1927, p. 100).

In a specimen of *C. excellens* the canal *Vm* (pl. 17) issues from the bottom of the brain-cavity slightly postero-medially to the canalis acusticus, and soon after its exit comes in close contact with this canal and is also for a short distance in open communication with it. The antero-median part of the labyrinth cavity is here transformed into a sharply defined groove (V_{3r}) for the r. mandibularis trigemini and this groove comes proximally in close proximity to the canal *Vm*, which is here only partly closed. In the *Cephalaspis* sp., figured in pl. 57, the canal *Vm* issues ventro-medially close to the fenestra acustica.

In *C. excellens* the canal *Vm* receives on its dorsal side and rather soon after its origin from the brain-cavity one (or two) minute canals from the same cavity (evidently corresponding to the canals *"Vx"* and *"Vxa"* in a *Cephalaspis* specimen described by Stensiö 1927, p. 101; cf. fig. 10 in this paper). In an unnamed *Cephalaspis* species (pl. 57:2-3) a short but not very narrow canal issues from the cavum cerebrale ventro-medially to the anterior part of the fenestra acustica and joins the canal *Vm* in the posterior third of its length.

The canal *Vm* is by Stensiö (1927, p. 106, *"Vd"*) considered to have transmitted visceral motor fibres of the n. trigeminus, and the same interpretation is adopted in this paper. We must, however, observe that the canal in question gave passage only to a part of the motor trigeminus, as another part is thought to have run through the canal V_3. It is thus worth noting that both these nerve roots must have issued from the medulla very close together, and that the conditions in a specimen of *C. excellens* (pl. 17), mentioned above, can be interpreted in such a way that there was a single motor root which soon after it had left the medulla divided into two branches, one running through the canal *Vm* and the other through the (groove and) canal V_3. It is here of considerable interest to notice the conditions in recent Myxinids with regard to the motor roots of the n. trigeminus (Allis 1903a, pp. 263, 274; Black 1917, p. 473, fig. 7; Holmgren 1919, fig. 27; Jansen 1930, pp. 368, 448, figs. 1—3, 56; Addens 1933, pp. 388—392, figs. 10—11; Lindström 1949, pp. 332, 346—353, figs. 9, 15). Two motor roots (several roots according to Allis) emerge from the ventral part of the cornu medullae to unite immediately into a common motor root. Soon after its passage through the membranaceous cranial wall the motor trigeminus divides into two main branches, one of which joins one of the sensory trigeminus branches while the other branch continues as a separate motor trunk. In *Petromyzon* (Ahlborn 1884, pp. 298—299, pl. 18; Johnston 1905a, pp. 151—155, pl. 5; Tretjakoff 1927a, pp. 381, 391—392, fig. 6; Addens 1933, pp. 365, 376—377, figs. 9, 50; Lindström 1949, pp. 366—370, 374, 393—395, figs. 24, 29—30, 36, 40) the motor roots are intimately joined to the sensory fibres and pass through the trigeminus ganglion. The conditions with regard to the motor roots are also much obscured by the fact that one of them has been interpreted as the n. abducens or as a n. oculomotorius-abducens (cf. besides the authors cited above, Cords 1929, pp. 213—214; Tretjakoff 1929; Stefanelli 1935; Woodburne 1936, pp. 413—417; Kappers 1947, pp. 75—76, pl. 1) but in this case the statements of the authors are most contradictory. Some small variations in the number of the motor roots of the n. trigeminus do occur but in general there are three roots, a small anterior one (composed of two or three small rootlets and regarded as the n. abducens or n. oculomotorius-abducens by some authors but definitely as a trigeminus root by Woodburne and Lindström), a large median root (considered by all authors to be a true trigeminus root) and a small posterior root (sensory root, Addens; possibly second abducens root, Stefanelli; at least to a major part belonging to the n. abducens, Lindström).

Returning now to the Cephalaspids, we have found one or two small canals from the cavum cerebrale joning the canal *Vm ("Vx", "Vxa"* Stensiö 1927, p. 101; *Vma* this paper pl. 57:2-3; cf. fig. 10). One of them or both are considered by Stensiö possibly to have given passage to the n. abducens (Stensiö 1927, p. 109, cf. p. 197). The nerve can possibly have followed this passage or it may have run through the canal *Vm* together with the visceral motor roots of the n. trigeminus, but it is impossible to say anything positive about it. In the latter case the small canals *"Vx"*, *"Vxa"*, *Vma* probably transmitted small rootlets of the motor trigeminus. Be that as it may, it seems, however, very probable that the n. abducens emerged through the cranial wall associated with the trigeminus motor roots (Stensiö 1927, p. 109) and not further forward through the canal lettered *"v. pt."* by Stensiö, as suggested by Allis (1931a, p. 515; cf. Stensiö 1927, p. 102). In this connection it can be pointed out that in fishes the n. abducens has its exit from the brain very far backward, at a level with the exit of the n. facialis or behind it (Herrick 1899, p. 385, pls. 15; 16; Norris & Hughes 1920, p. 313; figs. 20, 51; Kappers 1947, p. 118; pls. 2—3; figs. 67, 88, 91B, 93B; etc.).

The next canal in front is the one lettered *Vc* by Stensiö (1927, p. 101); it is seen in some specimens in the present material (pls. 14; 15:1; 17; 31:1; 57:2-3, *lat;* cf. fig. 10). In the *Cephalaspis* specimen used by Stensiö for his series A of sections (fig. 10; Stensiö 1927, p. 101; fig. 17; pls. 77—78; Holmgren & Stensiö 1936, fig. 214) the canal is followed backwards by a groove in the lateral wall of the cranial cavity towards the dorsal part of the fenestra acustica, and in *C. exilis?* (Stensiö 1927, series C of sections, pl. 93) it is continued within the trigeminus-lateralis chamber by a partly covered groove, which reaches on to the antero-lateral part of this chamber.

In *C. signata,* in the material now at hand, we can follow the canal *lat* to the cavum cerebrale. The corresponding posterior groove dorsal to the fenestra acustica can be traced backwards to the transition between the divisions of the cavum cerebrale which have lodged the cerebellum and the medulla oblongata (pl. 31:1, *lat).*

The canal was by Stensiö (1927, pp. 108, 197) thought to have given passage to the somatic sensory (general cutaneous) root of the n. trigeminus proper and also to certain visceral sensory fibres. As we have seen above, the anterior lateralis nerve must have run to the trigeminus-lateralis chamber or to the adjacent part of the orbit and not through the canal V_3. The anterior lateralis ganglion must thus have been situated in the said chamber or in its immediate vicinity in the orbit and its root fibres must have run through one of the canals connecting this chamber with the brain-cavity. Now we find the disposition of the structure lodged in the canal *lat ("Vc")* most similar to that of the root of the n. lateralis anterior in the Myxinids (Worthington 1906, pp. 170—172, figs. 1—3, 14; Holmgren 1919, fig. 27; Jansen 1930, pp. 368, 449, figs. 1—3, 56; Lindström 1949, pp. 355—357, 442, fig. 9), and hence I think it most probable that the canal *lat* really transmitted the root fibres for the lateralis anterior ganglion. This ganglion is thus supposed to have been situated in the antero-lateral part of the trigeminus-lateralis chamber (and possibly reached into the orbit in some species) and, accordingly, laterally or postero-laterally, but closely adjacent, to the trigeminus ganglion.

It can be observed that, to judge from the disposition of the groove in the posterior continuation of the canal *lat,* the roots must have run rather dorsally in the cavum cerebrale, and very probably on to the antero-dorsal part of the medulla oblongata, and it is thus of interest to note that this dorsal part in the Cyclostomes (and other lower vertebrates) contains the regio statica with the principal nucleus for the n. lateralis anterior (cf. Johnston 1902a, fig. 11; Ayers & Worthington 1908, p. 3, figs. 26, 30; Tretjakoff 1909, pp. 650—651; Pearson 1936, pp. 204, 216; Stefanelli 1937; Kappers 1947, p. 77, fig. 39; etc.).

It is of interest to notice that in *Petromyzon* the anterior preauditory lateralis ganglion which gives rise to the n. buccalis lies partly in front of the capsula auditiva and independent of the acustico-facialis ganglion complex and the posterior preauditory lateralis ganglion (for the lateralis nerve in the r. hyomandibularis; cf. Johnston 1905a).

Close to the opening of the trigeminus-lateralis chamber into the orbit, the chamber was found by Stensiö (1927, p. 101; series A—C of sections, pls. 78; 86—87; 92—93; cf. figs. 15—17, 23, *Vb;* Holmgren & Stensiö 1936, figs. 214—215, *Vb;* cf. this paper, fig. 10, *vcer)* in three *Cephalaspis* specimens to receive a canal on its dorsal side. The canal issues from the dorso-lateral part of the cavum cerebrale and runs in almost straight ventral direction to the trigeminus-lateralis chamber. In the specimen (of *C. exilis?)* in the series C of sections (pls. 92—93) a canal issues from the cavum cerebrale, runs for a short distance in lateral direction and then divides into a rather small antero-dorso-laterally directed branch *("IV")* and a somewhat larger one *("Vb")* which turns in ventral direction.

According to Stensiö (1927, pp. 108, 199) the canal *"Vb"* was traversed by general cutaneous (and communis) nerve fibres, constituting the sensory root of the n. profundus (and the canal *IV* gave passage to the n. trochlearis). Now we can see at once that this is a rather peculiar origin and course for a normal nerve root canal, and it seems a priori not very likely that it really contained such a structure. The suspicion that we have to do with some other structure is further strengthened by the conditions found in a couple of specimens in the present material.

In an unnamed *Cephalaspis* sp. (pl. 57:1, 3) we find a canal *(vcer)* issuing from the antero-dorsal part of the trigeminus-lateralis chamber near its opening into the orbit and running in dorsal and somewhat median direction. This canal is in communication with the cavum cerebrale by means of some short transverse canals ($vcer_1$, $vcer_2$, $vcer_3$, *IV?).* After the issue of the most dorso-median branch ($vcer_3$) the main canal *vcer* on the left side of the shield could be followed for only a short distance (as the shield is imperfectly preserved in this place) but it seems beyond question to have run to the dorsal face of the endocranium and here continued as a superficial supraorbital vein canal (cf. Stensiö 1927, fig. 23). On the right side of the same shield the fairly large opening of a canal is seen rather high up on the lateral wall of the cavum cerebrale (pl. 57:2, *IV, vcer)* posterior to the opening of the canal *III*. This foramen is regarded as the joint opening of the canals *IV* and *vcer*. Dorsally to this opening there is a short canal *(vcer)* piercing the roof of the cranial cavity and running in dorso-lateral direction to the dorsal face of the endocranium postero-medially to the orbital opening and there joining the canal *adsm* as it reaches the outer face of the endocranium (pls. 56:1; 57:2). From this place two small canals are starting in anterior, and anterior and slightly lateral direction (pl. 56:2); the median one of them is considered to be the anterior continuation of the canal *vcer* and to constitute a superficial supra-orbital vein canal (cf. Stensiö 1927, fig. 23).

The points of origin from the mesencephalic division of the cranial cavity of a pair of corresponding dorsal canals *(vcer)* are seen in *C. excellens* (pl. 15:2). The distal parts of the canals *vcer* are observed in *C. dissimulata* (pl. 8:1).

The canal *IV* is interpreted as being (and the canal *IV?* as possibly being) the canal for the n. trochlearis (cf. Stensiö 1927, p. 108; figs. 15, 17; pls. 78, 86—87, 92—93; Holmgren & Stensiö 1936, p. 254; figs. 214—215, 218; this paper, fig. 10), but the distal course of the canals could not be followed.

From what is said above it can be inferred that I regard the canal *vcer* and its branches as being the canal for a vein which drained at least some lateral and dorsal parts of the middle division of the cranial cavity, and in addition some superficial parts in the posterior portion of the inter-ocular space. On the left side of the shield (in pl. 57:1, 3) the vein was contained in a canal running mostly outside of the cranial cavity, but on the right side (pl. 57:2) the vein is thought to have entered the cranial cavity through the opening *IV, vcer* and then, for a short distance, to have run intra-meningeally in the cranial cavity, leaving the cavity through the dorsal canal *vcer*.

In *C. hastata?* a canal (pl. 33:1, *vcer)* separates from the canal for the post-orbital division of the v. capitis lateralis near its opening into the orbit, running in dorso-median and slightly posterior direction and reaching, as far as seen, with a small branch to the dorsal face of the endocranium, postero-medially to the orbital opening. The main canal, however, continues in medial direction, probably to the cavum cerebrale cranii. It is also possible that the canal *vcer* is developed in its ventral part only as a groove in the posterior wall of the orbit, originating at the opening of the canal *vcl*. This canal *vcer* in *C. hastata?* is considered to be homologous to the canal *vcer* in the *Cephalaspis* sp. above (pl. 57), but in this species, the origin of the canal *vcer* is thought to have shifted in lateral direction from the trigeminus-lateralis chamber to the canal *vcl* near its opening into the orbit. The canal *vcer* in *C. hastata?* thus contained a vein which opened directly into the

v. capitis lateralis. In the *Cephalaspis* species, considered above, the vein is thought to have passed through the opening of the trigeminus-lateralis chamber into the orbit and to have joined here the intra-orbital part of the v. capitis lateralis.

The canal ax_1, found by Stensiö (1927, p. 111) in *Kiaeraspis* and a *Cephalaspis* specimen certainly lodged a dorsal, extra-meningeal branch of a homologous vein.

With regard to the nature of this vein and its possible homologies in recent Cyclostomes and fishes it is evident that it must be considered as a cerebral vein, since it i. a. drained parts of the cranial cavity and entered the v. capitis lateralis as a median branch. It is not yet possible definitely to point out its equivalent in the Cyclostomes, since here, in the Petromyzonts, venous blood from the brain and cranial cavity is generally not found to run in closed vessels but in open peri-meningeal sinus, and the existence of cerebral veins other than the v. cerebralis posterior is positively denied by some authors (Gelderen 1924, pp. 546—548; cf. Daniel 1934, pp. 335—336; Towarnicki 1935). Sterzi (1907, p. 226), however, describes in adult *Petromyzon* veins, "vv. cerebrali medie", from the tela chorioidea mesencephalica, with irregular disposition, some of them leaving the cranial cavity in company with the n. trigeminus. The vein in question was in the Cephalaspids partly equivalent functionally to the v. cerebralis anterior in sharks (Parker 1887, pl. 35:8; Rex 1891, pl. 25; O'Donoghue 1914, fig. 2; Grodzinski 1938, fig. 19; 1946b, pp. 30—31, 37, 43—44, 62—63; figs. 2—7, 9—11; etc.) and to the v. cerebralis media in teleosts (Allen 1905, p. 84, v. cerebralis anterior = v. cerebralis media (spuria), cf. Gelderen 1924, pp. 558—561; Grodzinski 1946a, pp. 11—12, 15—17; figs. 2—4). In *Saurichthys* Stensiö (1925, p. 38) has observed a canal from the cranial cavity to the orbit which splits into two branches in its peripheral course through the orbito-temporal region. He interprets the canal as the common canal for the n. trochlearis and the v. cerebralis anterior, which distally passed separately, each through a canal branch of its own. The cerebral vein in the Cephalaspids, now considered, cannot, however, have been homologous to a v. cerebralis anterior or to a. cerebralis media (spuria) in fishes, since these veins always join the v. capitis lateralis (or medialis) in front of the n. trigeminus. With regard to its opening into the v. capitis lateralis in relation to the nn. trigeminus and facialis, it can possibly be compared with the v. cerebralis media in *Neoceratodus* (Gelderen 1924, pp. 561—562; cf. Grodzinski 1938, p. 41), but as this vein (and the v. cerebralis media spuria in Actiopterygians) leaves the cranial cavity in company with the roots of the n. trigeminus, the agreement between this vein and the cerebral vein in Cephalaspids is not complete. Thus, no direct homologies can be assumed between this cerebral vein in the Cephalaspids and any cerebral vein in the Gnathostomes. The vein in question is possibly homologous to the "vv. cerebrali medie" of Sterzi in *Petromyzon,* but nothing definite can be said about it.

The vein is here called the anterior cerebral vein (v. cerebralis anterior) and its canal the canal for the anterior cerebral vein, as opposed to the posterior cerebral vein, also present, but without thereby implying anything beyond a topographical designation.

In front of the canal *lat* there is in *C. excellens* (pls. 15:1; 17) another canal *(Vs)* running from the cavum cerebrale in antero-ventrolateral direction to the medial part of the trigeminus-lateralis chamber; this canal evidently corresponds to the canal "*Va*" in the series A and B of sections of the *Cephalaspis* specimens, described by Stensiö (1927, p. 102; pls. 78, 87, *v. pt.* (the canal *Va* in pl. 87:B 36 has beyond doubt transmitted only a small branch of the vein in the canal *Vb);* cf. figs. 16—17; Holmgren & Stensiö 1936, fig. 214; cf. fig. 10 in this papir, *Vs)* and probably to the canal "*v. pt*" in *C. exilis?* (series C, Stensiö 1927, pl. 89).

In the *Cephalaspis* sp. in pl. 57 we find in front of the inner opening of the canal *lat* two foramina in the wall of the cranial cavity, a rather large one *(Vs)* antero-dorsally to it and another much smaller one *(Vsa)* slightly ventro-medially to the opening *Vs,* and also in *C. signata* (pl. 31:1) we see in the postero-lateral wall of the trigeminus-lateralis chamber, antero-ventro-medially to the opening of the canal *lat,* two foramina, a larger one *(Vs)* and a smaller one *(Vsa),* the latter lying slightly antero-ventro-medially to the former. These two canals *(Vs, Vsa)* are regarded as corresponding to the single canal *Vs* in *C. excellens* and to the canal "*Va*" or its equivalent in the *Cephalaspis* species, described by Stensiö.

The canal "*Va*" is interpreted by Stensiö (1927, pp. 108—109) as having transmitted the supposed visceral motor root of the n. profundus. As we have found, however, that the canal "*Vb*" of Stensiö (= *vcer* in this paper) did not give passage to a nerve root but to a cerebral vein and as the canal "*Vc*" of Stensiö is here supposed to have transmitted lateralis root fibres, we have not yet located a canal for the sensory trigeminus roots.

In recent Cyclostomes the sensory root (or roots) of the n. trigeminus (and n. profundus) leaves the medulla antero-dorsally to the motor roots and anteriorly to the anterior lateralis root, and consists of one common root for the n. trigeminus and n. profundus or of one lateral and ventral root (or several rootlets) for the n. trigeminus proper and one median (and dorsal) root for the n. profundus (Ahlborn 1883, p. 211; pl. 13:2, 4, 6; 1884, p. 298; pl. 18:5-6; Retzius 1893, pl. 24:1-3; Allis 1903a, pp. 262—263; Johnston 1902a, p. 50; fig. 1; 1905a, p. 151; Worthington 1906, p. 164; figs. 1—2; Tretjakoff 1909, p. 671;

1927a, p. 381; Holmgren 1919, fig. 27; Cords 1929, pp. 217, 220, 222; Jansen 1930, p. 447; figs. 1—3, 57; Larsell 1947, fig. 1; Lindström 1949, pp. 332, 366).

The canal *Vs* in the Cephalaspids (or the canals *Vs* and *Vsa; "Va"* in Stensiö's descriptions) has the same topographical relations to the canals *Vm (Vm, Vma)* and *lat* as the sensory trigeminus root or roots to the trigeminus motor and the anterior lateralis roots in modern Cyclostomes, and it is, therefore, most natural to regard the canal *Vs (Vs, Vsa)* as having transmitted the sensory (general cutaneous) trigeminus root in the Cephalaspids. The roots of both the trigeminus and the profundus ganglion would then have run together in one canal in some *Cephalaspis* species but in others the roots in question were transmitted through two canals *(Vs, Vsa,* pls. 31:1; 57:2). As the canal *Vsa* leaves the cavum cerebrale medially to the canal *Vs* (it must, however, be noted, not anteriorly and not dorsally to it, but on level with the posterior part of this canal) and as it is the smaller one of these two canals, and since the n. profundus must have been much smaller than the sensory part of the n. trigeminus, it seems very probable that the (somatic-sensory) root fibres for the n. profundus ganglion were transmitted through the canal *Vsa.* The (somatic-sensory) root fibres for the trigeminus ganglion (g. gasseri) must consequently have left the cranial cavity through the canal *Vs.*

In the trigeminus-lateralis chamber the small profundus ganglion occupied an antero-median position, while the certainly much larger g. gasseri filled up most of the central part of the chamber and the anterior lateralis ganglion undoubtedly was situated laterally to these ganglia, in the antero-lateral part of the trigeminus-lateralis chamber.

We have finally yet another small canal from the cavum cerebrale cranii to the trigeminus-lateralis chamber to account for, and this is the canal lettered *"v. pt"* by Stensiö in his series A of sections (Stensiö 1927, p. 102; pls. 78—79; cf. figs. 16—17, 24; Holmgren & Stensiö 1936, fig. 214; cf. fig. 10, *v,* in this paper). From what has been said above it appears, that the canal *"v. pt"* in the series B and C of Stensiö (1927, pls, 87, 89, 91) is probably equivalent to his canal *"Va" (Vs* in this paper). The canal is found again in the present material in two *Cephalaspis* species *(C. excellens,* pl. 15:1; *Cephalaspis* sp., pl. 57, *v).*

In *C. excellens* (pl. 15:1) the canal *(v)* runs from the antero-dorso-median corner of the trigeminus-lateralis chamber in almost straight transverse direction to the cavum cerebrale, and is fairly wide. In the unnamed *Cephalaspis* sp. in pl. 57 the canal runs from the dorsal side of the chamber in dorso-medial direction and opens in the floor of the cavum cerebrale. On the left side the canal immediately beneath this floor gives off a small branch which opens slightly antero-dorso-laterally to the main opening of the canal (pl. 57:3, *v).*

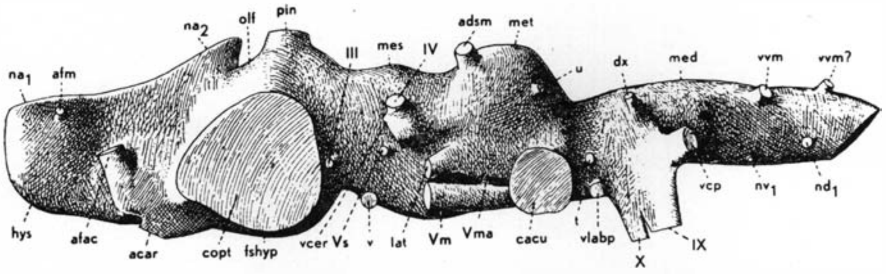

Fig. 10. — *Cephalaspis* sp. Cast of the cranial and ethmoidal cavity and the neural canal in lateral view. After Stensiö (Holmgren & Stensiö 1936, fig. 214), with lettering partly altered. About × 12.

acar, canal for the a. carotis (interna); *adsm,* canal for the postorbital superficial artery; *afac,* canal for the a. facialis; *afm,* canal for a median branch of the a. facialis for the outer part of the hypophyseal pouch; *cacu,* canalis acusticus; *copt,* canalis opticus; *dx,* canal for an artery to the posterior part of the dorsal sensory field; *fshyp,* hypophyseal fossa; *hys,* division of the ethmoidal cavity for the hypophyseal pouch; *lat,* canal for the roots of the n. lateralis anterior; *med,* most posterior part of the cranial cavity at the transition to the neural canal; *mes,* division of the cranial cavity for the mesencephalon; *met,* division of the cranial cavity for the cerebellum; *na*$_1$, anterior division of the naso-hypophyseal opening (opening of the hypophyseal pouch); *na*$_2$, posterior division of the naso-hypophyseal opening (nasal opening proper); *nd*$_1$, canal for the dorsal root of the first spinal nerve; *nv*$_1$, canal for the ventral root of the first spinal nerve; *olf,* division of the cranial cavity for the olfactory organ; *pin,* pineal canal; *t, u,* canals for vessels; *v,* canal for a vein, probably a branch of the v. cerebralis anterior; *vcer,* canal for the v. cerebralis anterior; *vcp,* canal for the v. cerebralis posterior; *vlabp,* canal for the v. posterior labyrinthi; *vvm,* canal for a vertebro-medullar vein; *vvm?,* canal possibly for a vertebro-medullar vein; *III,* canal for the n. oculomotorius; *IV,* canal for the n. trochlearis; *Vm,* canal for the motor trigeminus root passing to the r. maxillaris V; *Vma,* canal possibly for a motor trigeminus root; *Vs,* canal for the sensory roots for the nn. trigeminus and profundus; *IX,* canal for the n. glossopharyngeus; *X,* canal for the n. vagus.

The canal *v* (*"v. pt"*, Stensiö) I regard, following Stensiö (1927, pp. 102—103), as having been "traversed by a small vein which drained certain parts of the cavum cerebrale just at and posteriorly to the dorsum sellae and perhaps in addition also certain ventral parts of the mesencephalon and diencephalon". It most probably joined the anterior cerebral vein, mentioned above. I cannot, however, find it in any way homologous to the v. pituitaria (hypophyseal vein) in fishes (Stensiö 1927, pp. 103, 228; cf. Allis 1931a, p. 515, and as to the disposition of the v. pituitaria in fishes i. a. Allen 1905, p. 81; fig. 15; Allis 1914, pp. 228—246; 1919, pp. 221—222, 231, 275, 277; 1923, p. 152; 1928; de Beer 1924, pp. 296, 304, 317, 328; figs. 3, 7, 9, 11, 17, etc.; 1926, p. 270; figs. 4, 11, 14, 20, 26, 38, 39, 133, etc.; Goodrich 1930, pp. 239—241; figs. 245, 256, etc.). If such a vein was present, which is not very probable as it is wanting in recent Cyclostomes, it possibly went more anteriorly and from the left to the right orbit passing through the ventral part of the fenestra optica (cf. however Allis 1931a, p. 514, who denies the presence in *Cephalaspis* of a pituitary vein on the basis of the supposed absence of a v. capitis medialis).

Very little is known in detail of the trigeminus-lateralis chamber in cephalaspid genera, others than *Cephalaspis.* In *Nectaspis* (fig. 12; pl. 112:1), as said before, the chamber is lengthened and fusiform in shape and thus has its maximum breath in the middle of its length; postero-medially it rather gradually passes over into a wide canal *(rV),* connecting the chamber with the cavum cerebrale. In the basal part of the chamber and from its antero-median side issues a minute canal *(v),* running in median and slightly anterior and dorsal direction on to the cavum cerebrale. It is possible that all the trigeminus sensory roots and the roots of the ganglion laterale anterius and a part of the trigeminus motor roots (associated with the r. maxillaris) on each side left the cavum cerebrale through a common wide canal, just as they probably did in *Kiaeraspis* (Stensiö 1927, pp. 110—111). The canal *v* is very probably the canal of a vessel, but whether it transmitted an artery or a vein cannot be settled. It corresponds possibly to the vein canal *v* in *Cephalaspis,* just mentioned.

In this connection can be noticed that the real nature of the canal *"v. pt"* in *Kiaeraspis* (Stensiö 1927, p. 110; pls. 100—101; figs. 21—22) is very obscure. It has been interpreted by Stensiö as the canal for the v. pituitaria, but, according to what is said above on the canal with the same lettering in *Cephalaspis,* this seems not very likely, and the possibility cannot be set aside that it may have transmitted trigeminal motor roots, while the canal *"V"* transmitted general cutaneous and lateralis roots.

With regard to the other canals for nerves or vessels in the orbitotemporal region, viz. the canals for the nn. oculomotorius *(III)* and trochlearis *(IV),* the first nerve canal for the lateral sensory field *(sel_1),* branches of the postorbital superficial artery *(adsm),* supraorbital vein canals *(vso),* and those parts of the canal for the v. capitis lateralis *(vcl)* and its dorso-lateral branches *(vls)* falling in this region, I have nothing of general interest to add to the descriptions by Stensiö (1927, 1932) as only parts of them or only their proximal or distal openings are seen in the present material; some of them will, however, be mentioned in the following section on the otic region or in the chapter on the visceral endoskeleton.

Here shall only be cited what is said by Stensiö (1927, p. 120) concerning the canals *vso:* "Besides to veins certain of the canals *v. so_1—v. so_4* probably also gave passage to cutaneous nerve branches from the n. profundus. One of the posterior of these canals must obviously also have transmitted the lateralis nerve to the short transversal lateral line groove *(pc,* text-figs. 76, 77) situated close behind the pineal opening.". This latter sentence is of importance, and I can add that I have found no other canal through which a nerve for this sensory line could possibly have been transmitted. The sensory line in question must thus have been innervated by a nerve from the anterior lateralis ganglion (a r. ophthalmicus superficialis lateralis). The pineal sensory line in *Petromyzon* with which this line in the Cephalaspids has been homologized (Stensiö 1927, p. 238; 1932, p. 50; cf. Holmgren 1942, p. 7) is now known (Lindström 1949, pp. 389, 401, 442) to be innervated by the so-called r. postorbitalis glossopharyngei (from the posterior lateralis ganglion; see further p. 189 as to the consequences of these facts for the interpretation of the mentioned sensory line in the Cephalaspids).

The canal for the foremost part of the notochord, reaching forwards to the dorsum sellae, is seen in some specimens (pls. 8:2; 16:1; 39:1; 81:1; 83:2; 94:2, *ch).*

Before leaving the orbito-temporal region we shall only observe that in *C. signata* (pl. 31:2, *pin)* the pineal canal is very wide and long; it must obviously have enclosed not only the pineal body, epiphysis (and paraphysis), but also a well developed saccus dorsalis (cf. *Petromyzon,* Sterzi 1907, fig. 18; Herrick & Obenchain 1913, figs. 1—2; Saito 1930, figs. 1—4; Heier 1948, figs. 1—2).

The otic region. The canals for the roots of the trigeminus (s. l.) and the anterior lateralis nerves, which pierce the otic region, have been dealt with above in connection with the trigeminus-lateralis chamber or with the parts of them which run in the orbito-temporal region. We have thus seen that the root of the r. mandibularis V in general left the cranial cavity proper through the most anterior part of the so-called fenestra acustica and went for a short distance in a well marked groove in the antero-medial wall of the labyrinth cavity in order finally to enter a canal of its own.

The term fenestra acustica is here used for the large opening between the cavum cerebrale cranii and the labyrinth cavity, which is thought to have transmitted the proximal part of the r. mandibularis V, the roots of the nn. VII and VIII, and the roots of the nerves for the sensory fields, and possibly some vessels. The connecting part between the cavum cerebrale and the labyrinth cavity is often lengthened to form a short canal, which then may be called the canalis acusticus; it corresponds to the acustico-facialis canal of Stensiö (1927, p. 72). The fenestra *(facu)* or canal *(cacu)* in question is seen in several specimens (pls. 3:1; 4; 14; 15:1; 16—17; 39:1; 40:3; 57:2-3; 112:1).

The fenestra acustica was by Stensiö (1927, pp. 71, 193) thought to have transmitted only a part of the n. acusticus, namely an anterior branch, which must have corresponded to the r. utricularis VIII in recent Cyclostomes. The posterior branch of the n. acusticus, r. saccularis VIII, had passed, according to Stensiö (1927, pp. 71, 81, 192), through a canal of its own, which leaves the cavum cerebrale some distance behind the fenestra acustica and goes to the postero-median part of the labyrinth cavity, ventrally to the division of that cavity for the ampulla posterior (Stensiö 1927, figs. 15—22, 24, 28; pls. 25—26, 49, 50, *VIIIp;* Holmgren & Stensiö 1936, figs. 213—215, 217, 219, *VIIIp;* cf. this paper, fig. 10, *vlabp).*

In the present material a corresponding canal is observed only in a few specimens, as e. g. in a specimen of *C. acuminata* and of *C. signata* (pl. 31:6, *vlabp).* In an unnamed *Cephalaspis* species there exists on the right side an opening into the cavum cerebrale (pl. 57:2, *vlabp)* which I regard as the inner opening of this canal. It must be observed that the opening lies rather far behind the fenestra acustica. There exists, however, definitely no such opening on the left side (pl. 57:3).

In the specimen of *C. excellens* figured by Stensiö (1927, pls. 25—26, *"C. vogti?"),* which I have examined, the canal *"VIIIp"* issues from the basal part of the vagus canal *("IX + X + Xv. cp")* and runs on the left side in lateral and slightly posterior direction along the posterior margin of the division of the labyrinth cavity for the ampulla posterior. For a short distance it is in open communication with this cavity but farther distally forms again a closed canal; the distal part of the canal is fractured and could not be followod. From the course of this canal it is evident that it could not have transmitted a branch of the n. acusticus, and if the canal really is homologous to the canal with the same lettering in other species, it follows that neither in these species can it have lodged a n. acusticus branch. In favour of this view is also the fact that the canal in the *Cephalaspis* sp. mentioned above (pl. 57:2, *vlabp)* opens rather far behind the fenestra acustica (the r. posterior VIII would have lain far apart fram the r. anterior VIII, which is not the case in modern Cyclostomes and fishes) and that it is lacking on the left side. It can also be noted that the canal in some specimens of *Kiaeraspis* (Stensiö 1927, pls. 49—05) is much too large for a branch of the acusticus nerve. It can furthermore be noticed that the subdivision into two separate nerves of the n. acusticus in the Myxinids, with which the Cephalaspids in this respect have been compared (Stensiö 1927, p. 142), very probably is connected with the peculiar structure of the labyrinth organ in these Cyclostomes (cf. Ayers & Worthington 1908, p. 10).

As to the transmission of any branch of the n. acusticus by the canal *"VIIIp"* we can say on the whole that this is certainly not the case in some Cephalaspids, while in others there exists a very great probability against it. All the roots of the auditory nerve are thus thought to have run through the fenestra acustica and very probably soon to have formed a ganglion acusticum from which the branches of the n. acusticus for the different parts of the membranous labyrinth took their origin.

If the canal *"VIIIp"* did not transmit a branch of the acusticus nerve we must find for it another interpretation. That it gave passage to a nerve seems most improbable. Judging from its position in relation to the vagus canal and under the assumption that the small canal *t* (fig. 10; pls. 30:3; 57:2-3; cf. Stensiö 1927, pp. 71, 81; figs. 15—18; pl. 55) dorsal to it enclosed a branch from the a. encephalica posterior, we can with some probability surmise that the canal in question transmitted a vein, which drained some posterior parts of the membranous labyrinth and possibly some other structures in the labyrinth cavity, in order to empty into the v. cerebralis posterior within the brain-cavity. This supposed vein is here called the v. posterior labyrinthi and its canal the canal for the v. posterior labyrinthi.

We can find analogous conditions in fishes: in *Scyliorhinus* (= *"Scyllium")* the veins from the membranous labyrinth are said apparently to open into the posterior cerebral vein at its inner end (O'Donoghue 1914, p. 442), and in *Ophiodon* a posterior auditory vein from the ampulla posterior empties into a branch of the posterior cerebral vein (an anterior auditory vein from other parts of the membranous labyrinth joins the v. cerebralis media spuria, Allen 1905, pp. 84, 86; fig. 25).

Openings into the cavum cerebrale, corresponding to the canals *t* in *Cephalaspis* sp. and *Kiaeraspis,* and *u* in *Cephalaspis* sp. and *C. exilis?* described by Stensiö (1927, pp. 71—72, 81, 83) are found in an unnamed *Cephalaspis* sp. (pl. 57:2-3), and the canal *t* is seen also in *C. signata* (pl. 30:3). In this species it is observed (not figured) that the canal after its opening into the labyrinth cavity, or more exactly, into that part of the cavity which lodged the nerve for the dorsal sensory field and the otical vein[1] is continued by a groove in dorsal direction and eventually in a dorso-lateral direction to that part of the labyrinth cavity which lies between the canal *des* and the commissural division; there it splits into two small branches. As mentioned above, the canal *t* possibly transmitted a branch from the posterior encephalic artery, and the canal *u* certainly gave passage to a vessel (Stensiö 1927, p. 83) but as to the nature of this vessel I can give no definite opinion.

The canal *adsm* (fig. 10; Stensiö 1927, pp. 72—73, figs. 15—17, 20—23, 25—27; Holmgren & Stensiö 1936, figs. 213—215, 218)

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[1] In *C. signata* the canal *des* for this nerve has a somewhat more posterior position and a more postero-median course than in the *Cephalaspis* sp. and *Kiaeraspis,* described by Stensiö (1927, figs. 18—19).

from the dorso-lateral part of the cavum cerebrale to the superficial parts of the otic and the orbito-temporal regions, interpreted as a canal for the a. postorbitalis superficialis (Stensiö 1927, pp. 73, 212), is seen in several specimens in the present material (pls. 8:1; 10:2; 11:4; 13; 15:2; 24:2; 30:3; 31:1-2; 36:2; 56:1; 57:2-3; 77:2; 106—107, *adsm).* In *C. signata* (pls. 30:3; 31:1-2) two or three branches are also given off from the main canal for the superficial postorbital artery to the postero-median part of the orbit. In the same specimen the canal is seen to open comparatively far backwards and into the posterior part of the division of the cavum cerebrale for the cerebellum *(met),* and to be continued in ventro-median direction by a short groove in the posterior wall of this division (pl. 30:3). From the disposition of the canal and the connected groove in this species it seems very probable that the artery which was lodged in them was a direct dorsal continuation of the artery (a. encephalica posterior) which passed through the canal *cpost* in the occipital region.

The large canal for the postorbital division of the v. capitis lateralis *(vcl)* which traverses the dorso-lateral parts of the otic region is more or less well displayed in many specimens (pls. 4:1; 5:3; 8:2; 10; 11:4; 13—17; 30:3; 31:1, 2, 4; 32:3; 33:1; 56:1; 62:1; 63:2; 64:2; 68:3; 77:2; 93:2). The canal leaves the orbit at its postero-dorso-lateral corner and runs in straight posterior direction, as in *C. excellens* (pls. 13—15; 17) and *C. signata* (pl. 32:3), or slightly sigmoidally bent in *Hoelaspis angulata* (pl. 77:2; cf. Stensiö 1927, pls. 45; 47:1), or more distinctly so in *Boreaspis curtirostris?* (pl. 93:2). In other species the canal issues from the postero-dorsal corner of the orbit and travels straight backwards *(C. heintzi,* pl. 5:3, and *C. exilis,* pl. 11:4) or with a slight median bend *(C. hoeli,* pl. 10:2; *Securiaspis,* pls. 62:1; 63:2; 64:2). In *Boreaspis curtirostris?* (pl. 93:2) the canal *vcl* is found to be in open communication with the labyrinth cavity.

During its course through the otic region the canal for the v. capitis lateralis receives some small branches from the superficial parts of the region and from the labyrinth cavity (Stensiö 1927, pp. 76, 225), and, on its lateral side, some generally large canals coming from the superficial dorso-lateral parts of the visceral endoskeleton. The former canals have not been observed at all or only as small fragments in the material now at hand and will not be dealt with here, the latter will be treated in the chapter on the visceral endoskeleton. Here will only be noted that in *Nectaspis areolata* a couple of superficial canals is found posteriorly to the orbit (pls. 106—107). In this species vascular canals are much anastomosing, in some places to such a degree as to form an irregular network of canals, in which the course of the individual main canals can be disentangled only with considerable difficulty. The anterior one *(vds)* of the canals probably corresponds to one of the canals "*v. ds*$_1$" and "*v. ds*$_2$" in *Cephalaspis* (Stensiö 1927, figs. 23, 25—26) or to the canal "*v. ds*" in *Kiaeraspis* (Stensiö 1927, fig. 27), and the posterior one *(ads)* possibly runs to the dorso-lateral part of the labyrinth region and represents a canal for an artery to the dorso-lateral superficial parts of this region; proximally this artery would then have issued from the anterior part of the a. communicans (see below, p. 97). The canal *vds* is a canal for a vein from the dorsal part of the otic region.

A major part of the otic region is occupied by the rather spacious labyrinth cavity; it is lined with a perichondrial bone-layer of its own, which directly or by means of canal bone-layers is primarily continuous with the cerebral division of the cranial cavity (Stensiö 1927, p. 77). The labyrinth cavity can be divided into two distinct parts, a mainly ventro-lateral one, consisting of the so-called vestibulum, and another one, mainly dorso-median, comprising the two vertical semicircular divisions (one anterior and one posterior division) and the commissural division (see also Stensiö 1927, pp. 77—94; Holmgren & Stensiö 1936, p. 256).

From what is seen of the labyrinth cavity in the specimens among the present material it is evident that it is built on the whole like that in the *Cephalaspis* sp. and *Kiaeraspis,* described by Stensiö (1927). We shall only point out here some structural details which are regarded as being of special significance.

The vestibular division *(vest)* of the labyrinth cavity is well exposed in many specimens (pls. 3:2; 4; 8:2; 9:4, 7; 13—14; 15:1; 16—17; 29:2; 30:3; 31:1-3, 6; 32:1-2; 33:1; 39:1; 40:3; 71:3; 81:1; 82:1, 3; 93:2; 94; 112:1). One or both of the semicircular divisions *(csema, csemp)* or parts of them *(ampa)* are seen in several specimens (pls. 11:4; 13—15; 16:1; 17; 31:1; 33:1; 56:1; 64:2; 68:3; 77:2; 92:5; 93:2; 95:1), and also the commissural division *(com)* is observed in some specimens (pls. 13; 15:2; 30:3; 33:1; 56:1; 77:2).

It is definitely established by Stensiö (1927, p. 80) that the membranous labyrinth in the Cephalaspids must have resembled most closely that of recent Petromyzonts and have been fundamentally distinct from the type found in fishes and higher vertebrates in having only two (vertical) semicircular canals and lacking the horizontal one.

By closer comparison between the labyrinth cavity in the Cephalaspids and the membranous labyrinth in the Petromyzonts (see Retzius 1881, pp. 13—27; Krause 1901, pp. 104—105; 1906; Burlet & Verstegh 1930, pp. 8—44; Burlet 1934, pp. 1300—1302; etc.) we find, however, distinct discrepancies which make it certain that the membranous labyrinth in the Cephalaspids differed rather much from this latter. It is thus evident that the labyrinth in the Cephalaspids, although built on the same basis as that of the Petromyzonts, had the “ciliated rooms” (vestibulum), if they were present at all, very slightly developed and devoid of their upper divisions. The development of the semicircular divisions, furthermore indicates that the ampullae of the simicircular canals were, most probably, simple and not trifid and thus without any sinus ampullae utriculares. The structure of the utriculus, into which the two ampullae opened, is unknown, and whether or not there were any ventral recesses, corresponding to the lagena and sacculus, is undecided; neither can the place of origin of the ductus endolymphaticus (if from the utriculus or from the crus commune) be determined. From the comparison it appears that the membranous labyrinth in the Cephalaspids very probably only occupied a dorso-median space in the labyrinth cavity, and that the vestibular division mostly enclosed structures others than the labyrinth. This latter assumption is also based on other facts as we shall see in the following.

In the figures of casts of the labyrinth cavity of *Cephalaspis* sp. and *Kiaeraspis,* given by Stensiö (1927, figs. 18—19; Holmgren & Stensiö 1936, fig. 217) we can observe that the vestibular division has a large and fairly distinct oblong swelling proximally to the exit of the first nerve canal for the lateral sensory field *(“*sel_1, $_2$*”).* In *C. acuminata* this swelling is well marked (pl. 3:1, $gsel_1$), and in *C. signata* it is strongly developed and partly separated from the rest of the vestibulum, forming an antero-median division of this part of the labyrinth cavity (pls. 31:1-3; 32:1-2, $gsel_1$) or, expressed in another way, the proximal part of the canal sel_1 in *C. signata* is distinctly widened and this enlarged part of the canal communicates with the antero-median division of the labyrinth cavity. In some *Boreaspis* species at least the lateral part of the floor of the vestibulum is provided with some distinct but small transverse ventral protuberances (pls. 81:2; 83:1; 94:2, *gsel)* from which issue, in dorso-lateral direction, the nerve canals for the lateral sensory fields. In a specimen of *C. excellens,* in which the floor of the left vestibulum has been cleaned from the inside, we find that this floor is furnished with at least two transverse partitions (pl. 16:1, *pg),* dividing the basal part of the vestibulum into three basal chambers, of which the middle one, lying medially to the inner opening of the canal sel_4, is fusiform in outline and well displayed (in pl. 16:1, $gsel_4$).

It is quite clear that the basal swelling of the canal sel_1 in *C. signata* can only have been caused by a ganglionic structure from which the nerve in this canal arose. From this follows that the swellings and the ventral protuberances or the basal chambers of the vestibular division of the labyrinth cavity, referred to above, also without any reasonable doubt partly lodged the ganglion of respective nerve for the lateral sensory field, and that the basal chamber $gsel_4$ in *C. excellens* thus lodged the basal parts of the ganglion of the fourth nerve for the lateral sensory field. It seems furthermore very probable that these ganglia were large and occupied a major part of the vestibular division of the labyrinth cavity.

If, as assumed, the nerves for the lateral sensory fields issued from ganglia (lying in the vestibulum) it follows, of course, that also the nerve for the dorsal sensory field took its origin from a ganglion. No definite opinion as to the place of this ganglion within the labyrinth cavity can, however, be advanced.

The hypothesis that the nerves for the areas, which in this paper are called the sensory fields ("electric fields", Stensiö), were ganglionic in their proximal ends has a definite bearing upon the question as to the nature of these nerves and consequently also upon that of the nature of the fields which they innervated. This latter problem will be discussed later (p. 192); here we shall only stress the fact that the nerves in question undoubtedly must have been sensory nerves.

The designation "vestibular division of the labyrinth cavity" is, strictly speaking, not appropriate if it implies that this division contained a structure corresponding to the so-called vestibulum ("ciliated rooms") in the Petromyzonts (Stensiö 1927, p. 80); the name vestibulum or vestibular division is, however, here retained as a noncommittal term for the large latero-ventral room in the labyrinth cavity.

From the lateral part of the vestibulum issue several canals, viz. five large nerve canals for the lateral sensory field (or fields, sel_1—sel_5), the canals for the posterior (motor) trunk of the n. trigeminus (r. mandibularis V, V_3), the n. facialis *(VII),* most often the n. glossopharyngeus *(IX)* and most often also the so-called a. communicans *(acom),* the two latter often in a common canal *(IX + acom).* These two latter structures generally traversed the postero-lateral part of the vestibulum and thus have each a separate posterior opening or a common posterior opening through the posterior wall of the vestibulum. In addition there are usually some openings of canals for dorso-lateral superficial arteries *(ala, alp)* into the vestibular division. Connected with the vertical commissural division of the labyrinth cavity there are a dorso-median canal for the nerve of the dorsal sensory field *(des),* a posterior canal for the otical vein *(vdsv),* and a small canal connecting the canal *vdsv* with the brain-cavity *(dx).* For a comprehensive account of these structures the reader is referred to the papers by Stensiö (1927; Holmgren & Stensiö 1936).

The very exit from the labyrinth cavity of the canals for the dorso-lateral superficial arteries has not been observed in any specimen in the present material except in *C. oreas* (pl. 8:2), where the canal for a dorso-lateral artery *(ala)* is seen leaving the vestibulum and running in dorso-lateral direction to the outer face of the endoskeleton, and in *C. excellens* (pl. 16:2, *alp).*

The origin of the canal for the n. facialis *(VII)* is seen only in *C. signata,* in which it leaves the cavity together with the canal *sel*$_2$ and anterior to it (pl. 32:1; cf. Stensiö 1927, figs. 18—19, 23—25, 27).

Those canals in the otic region which have not yet been considered will be dealt with in connection with the canals of the occipital region or of the visceral endoskeleton.

The occipital region, as here delimitated, is very short and broad; anteriorly it passes into the otic region, and is continuous posteriorly with the inter-zonal endoskeleton and laterally with the zonal endoskeleton (the endoskeletal shoulder-girdle). It has no free lateral borders. Ventrally the anterior part of the region passes over into the postbranchial wall of the visceral endoskeleton, which abuts against the endocranium at the transition between the occipital and otic regions, while the posterior part of the region has a free ventral face.

The most conspicuous of the canals in this region is the vagus canal, but there are also many other important canals which will be dealt with before we give an account of the vagus canal and the canals associated with it, the vagus canal complex.

The large and short canal *vdsv* (referred to above), which transmitted a vein, the otical vein, considered to have drained a middle part of the dorsal sensory field and certain parts of the labyrinth cavity, and also to have given passage to the ductus endolymphaticus, soon joins the large occipital vein sinus (Stensiö 1927, pp. 64, 74, 85, 230; figs. 18—19, 23, 26—27; Holmgren & Stensiö 1936, figs. 217—218). The canal *vdsv,* but only its proximal part near the junction with the canal *des* and the commissural division of the labyrinth cavity, is seen in a few specimens in the present material, viz. in *C. excellens* (pls. 13; 15:2), *C. hoeli* (pl. 10:2), *C. signata,* and an undetermined *Cephalaspis* sp. (pl. 57:2).

Parts, and mostly anterior parts, of the large occipital vein sinus (cf. Stensiö 1927, p. 61; figs. 23—27; Holmgren & Stensiö 1936, p. 262; fig. 218) are observed in some specimens (of *C. acuminata,* pl. 3:2; *C. excellens,* pls. 13, 15, 17, and *Cephalaspis* sp., pl. 56, *vsoc),* and its connections with the canal of the v. capitis lateralis and with the canal of the v. cerebralis posterior are exposed, the former in *C. hoeli* (pl. 10:2), both in *C. excellens* (pl. 17) and the latter connection also in *Cephalaspis* sp. (pl. 56:1-2).

The v. cerebralis posterior issued in *Cephalaspis* from the brain-cavity together with the roots of the metotic cranial nerves in the big vagus canal (Stensiö 1927, pp. 52—53; figs. 15—17, 24). In *Kiaeraspis* (Stensiö 1927, figs. 20, 22) the vagus canal is very short and indistinct and the vein in question passed through an almost independent canal from the cranial cavity.

In an unnamed *Cephalaspis* sp. the v. cerebralis posterior of the left side issued from the brain-cavity through a very short vagus canal (pl. 57:3, *vc),* but left the cavity on the right side through a canal of its own, distinctly postero-dorsally to the canal $IX+X$ (pl. 57:2, *vcp).*

As is known (Stensiö 1927, pp. 62, 86), the ductus endolymphaticus must have passed from the labyrinth cavity through the canal for the otical vein, the median part of the occipital vein sinus, and finally in a short canal from the postero-median corner of this sinus in order to issue through a foramen on the postero-dorsal side of the cephalic shield. The opening of the canal (d_1) on the dorsal face of the endoskeleton or in the exoskeleton is observed in many species of *Cephalaspis,* in *Securiaspis, Ectinaspis, Benneviaspis, Hoelaspis, Boreaspis, Kiaeraspis, Axinaspis* and *Nectaspis* (pls. 5:3; 6:1; 8:1; 9:2; 10; 11:3-4; 19:1; 24; 25:2; 36:2; 39; 44:2; 46:2; 49:1; 51:1; 61; 63:2; 64:2; 67:2; 68:3; 69; 70:2; 71:3; 73—74; 76:1; 77:2; 78:3; 91:1; 97:1; 100:3; 106). The canal also transmitted a vein from the postero-dorsal superficial parts of the cephalic shield. The canal for this vein will be further dealt with below (p. 113), together with some other vein canals, which join the occipital vein sinus.

The small canal *dx* (cf. Stensiö 1927, pp. 57, 81, 86; figs. 15—20, 22—23; Holmgren & Stensiö 1936, figs. 214—215, 217—218; this paper, fig. 10) from the brain-cavity to the most proximal part of the canal *vdsv* is observed in some *Cephalaspis* species (pls. 13; 15:2; 29:3; 57:2-3). As the canal *dx* generally joins the canal for the otical vein *(vdsv),* its most obvious interpretation seems to be that it transmitted a vein. Stensiö (1927, p. 86, cf. p. 192), however, regards it as having given passage to an artery or to a nerve or to both these structures. Judging from the conditions in a specimen of *C. signata* I think it most likely that it really transmitted an artery and not a vein. In the specimen in question the opening of the canal *dx* on the left side into the canal *vdsv* (or, more precisely, into the common canal for the otical vein and the nerve for the dorsal sensory field) is continued by a groove which runs for a short distance in dorsal direction to that dorsal part of the common canal which is thought to have transmitted the nerve for the dorsal sensory field, and this groove is considered to have lodged the continuation of the artery running through the canal *dx.* On the right side of the same specimen the canal *dx* is replaced by some small canals from the canal *adspd* (which gave passage to an artery for the dorsal spine, see below; cf. pl. 30:4).

More or less on the same transverse level with the opening from the cavum cerebrale of the vagus canal and the canal *dx* the floor of the cranial cavity is pierced by a pair of foramina, openings of short canals *(cpost)* to this cavity from the aortal groove (or canal), transmitting the a. encephalica posterior (the occipital encephalic artery, Stensiö 1927, pp. 56—57, 213). One of them or both, normally developed, are exposed in some species of *Cephalaspis* (pls. 9:7; 14; 15:1; 16; 39:1, 3; 57:2), in *Boreaspis costata* (pl. 86:2) and *Nectaspis areolata* (pl. 112:1).

In some *Cephalaspis* species we find, however, aberrant conditions with regard to this canal in rapport with the development of special structures which will now be described.

In *C. hastata?* there is observed on the right side a double foramen in the roof of the aortal groove (or canal) or, more exactly, a small median opening and immediately lateral to it a much larger one (pl. 33:1, *cp).* This opening is seen to lead into a wide canal *(adspd),* which, bending in a postero-dorso-median direction, runs entirely outside of the division of the cranial cavity for the medulla oblongata. Immediately after its origin the canal gives off a very small canal in median and slightly dorsal direction, probably to the cavum cerebrale. After a short distance the canal *adspd* receives a tributary *(adsps)* which opens into the left side of the canal and this is beyond doubt a canal from the left side, corresponding to the canal *adspd.* After the junction of the canals *adspd* and *adsps* the resulting common canal *adsp* soon takes a median position and runs in a straight posterior direction, lying dorsally to the neural canal (it thus enters the inter-zonal endoskeleton but its posterior part is not preserved; pl. 32:4). At about a level with the openings of the ductus endolymphatici the canal *adsp* gives off a branch from its ventral side *(adspx),* which runs for a short distance in posterior direction on the right side of the canal *adsp* and sends out small branches, i. a. to the superficial dorso-lateral parts of the dorsal inter-zonal endoskeleton.

In a specimen of *C. signata* the exit of the large canal *adspd* from the right side of the aorta groove is seen in pl. 31:2 *(adspd);* the canal first runs in postero-dorsal direction and then turns in postero-dorso-medial direction and receives the canal *adsps* (pl. 29:3) which in this species issues from the right dorso-lateral side of the medullar division of the cranial cavity. The common canal *adsp* continues in postero-dorso-medial direction until it reaches the median line of the shield (the distal part of the canal is not preserved). The canal *adspd* gives off from its dorsal side some small and short canals which lead to the canal *(des)* for the right nerve to the dorsal sensory field; in this connection it is to be noted that the canal *dx* is wanting on the right side but present on the left side (pl. 29:3).

In *C. doryphorus* (pl. 39:1, 3-4) the left canal *cpost* is somewhat enlarged; immediately after its entrance into the endoskeleton it gives off a strong lateral branch, which is the canal *as* (to be accounted for later on, p. 97), and then enters the cavum cerebrale somewhat behind the origin of the vagus canal. Slightly behind a transverse level through the posterior opening of the canal *Xl* a strong canal *(adsp)* leaves the neural canal in the median line of the dorsal side. Between the opening of the canal *cpost* into the cavum cerebrale and the exit of the canal *adsp* the wall of the cavum cerebrale and of its posterior continuation, the neural canal, shows a fairly distinct groove, which indicates that the structure in the canal *cpost* continued backwards and entered the canal *adsp*. The canal *adsp* runs backwards and enters the antero-ventral part of the dorsal spine. Slightly behind its origin it gives off a small branch *(a_1)* to the neural canal and also a branch *(a_2)* in lateral direction.

In an undeterminable *Cephalaspis* specimen (pls. 56:1-2, 4; 57:2) there is on the dorsal side of the hindmost part of the cavum cerebrale an opening (pl. 56:1-2, *adsp)* which leads into a long canal running in posterior direction in the median line dorsally to the neural canal or groove; (it will be further described in the chapter on the inter-zonal endoskeleton, p. 110).

In *C. excellens,* finally, there is also a corresponding canal (pl. 15:2, *acrl)* but which issues from the neural canal further posteriorly than in the now described species. It will be accounted for in connection with the canals from the neural canal.

As the canal *adsp* in some species arises from the aortal groove (or canal) and as in others it is distinctly connected with the canal *cpost* for the a. encephalica posterior, it must have transmitted an artery, and, more precisely, an artery for the dorsal spine (see below on the canals of the dorsal spine). The artery and its canal will be called the a. spinae dorsalis and the canal for the a. spinae dorsalis, respectively. The canal is evidently serially homologous to a canal for a posterior artery for the dorsal spine in *C. doryphorus,* and homologous to the canal *acrl* in *C. excellens* (cf. Stensiö 1927, pp. 56—57). The artery in the canal *acrl* may be called the a. cristae (longitudinalis) dorsalis.

In *C. hastata?* the lateral opening *(cp)* thus leads into the canal for the a. spinae dorsalis, and the small opening medially to it is probably the real opening for the a. encephalica posterior.

As the (left) canal *as* (for the occipital segmental artery, see below, p. 97) in *C. doryphorus* issues as a branch from the (left) canal *cpost* it seems probable that the arteries in both these canals belonged to the same morphological unit, having been the lateral and dorsal branch, respectively, of a segmental artery (cf. Stensiö 1927, pp. 56—57, 358, 365, who interprets the posterior encephalic artery as a transformed segmental artery).

We shall now turn to the vagus canal and its proximal branches and some canals connected with them, and first consider a specimen of *C. signata* in which these structures are most complete and most complicated (fig. 11; pls. 29:2; 30:3; 31; 32:1-2). Before proceeding we can notice that the dorso-medial part of the postbranchial wall is well developed and that the occipital region reaches somewhat more posteriorly in this specimen (as also in some specimens of other species) than in the specimens studied by Stensiö (1927), in such a way that most of the canal complex, just mentioned, is enclosed in the endoskeleton. In the specimens studied by Stensiö (1927, pp. 52—56; figs. 13—14; pls. 75; 84—85; 92—96; 100) the nerves and vessels in this complex lay partly behind the endocranium and the postbranchial wall, causing grooves and pits on their posterior face.

As mentioned above, the canal for the v. cerebralis posterior mostly joins the dorsal part of the vagus canal; this part will not be considered here.

The rather short vagus canal *(vc.* pl. 31:4-5; fig. 11) is very wide, and forms a fairly spacious chamber, which must have lodged the ganglia of the n. glossopharyngeus, the n. vagus and the n. lateralis posterior, since after the branching of the vagus canal into fairly uniform and narrow canals there are no more distal places, where the ganglia could have been situated (cf. Stensiö 1927, pp. 190—191). We find thus, contrary to what is the case in the trigeminus-lateralis-anterior-complex, that the ganglia of the metotic cranial nerves lay closely to the cavum cerebrale and that all the roots to these ganglia passed from the cavum cerebrale through a single common canal.

The most proximal part of the vagus canal receives from below two short and narrow canals, being branches of a common very short trunk issuing from the dorsal side of the aortal groove. The opening into the vagus canal of the posterior branch is the larger one and lies directly behind the anterior one, as seen in pl. 31:4 *(a).* The canals most certainly transmitted small arteries from the aorta to the metotic ganglion complex.

Near the base of the vagus canal and from its postero-medial part, shortly behind the opening of the posterior canal *a,* there issues a fine canal *vvma* (pls. 31:4; 32:1) which runs in postero-lateral direction and soon joins a small posterior canal *(vvmb)* coming from the ventro-lateral side of the neural canal. The common canal (vvm_1) thus formed runs in its turn in the same direction as the canal *vvma* but also slightly upwards to the median side of a longitudinal fairly small canal *(vct)* with which it unites. The further description of these and other canals, connected with the neural canal in its anterior part, and with the occipital vein sinus, will be postponed to the chapter on the inter-zonal endoskeleton, in which also an interpretation of all of them will be attempted.

Laterally to the exit of the canal *vvma* there issues from the postero-dorso-lateral part of the vagus canal a fairly narrow canal

(Xl, fig. 11B—C; pl. 31:4) which runs, meandering very slightly and without apparent branches, in an almost straight posterior direction backwards into the inter-zonal endoskeleton. From is disposition and the nature of its course the canal *Xl* must be a nerve canal and in that case it can only have transmitted a branch of the n. lateralis posterior or the main r. lateralis vagi (with regard to this nerve canal in other species see farther below in the chapter on the inter-zonal endoskeleton, p. 115).

Immediately lateral to the origin of the canal *Xl* a minute canal *(v,* fig. 11B; pl. 31:4) runs from the vagus canal in postero-dorso-lateral direction to the occipital vein sinus; the canal possibly transmitted a vein.

As is known from the description of *Cephalaspis* sp. by Stensiö (1927, p. 52) the short vagus canal generally breaks up into three main canals. The branch corresponding to the canal *IX* (fig. 10; Stensiö 1927, p. 53; figs. 15—17, 24, 26; Holmgren & Stensiö 1936, fig. 215) will now be treated.

The canal *IX* issues from the vagus canal in straight lateral direction, and, after having run for a short distance, divides into two branches, IX_1 and *IXl* (pl. 31:4-6). The latter canal *(IXl)* continues in lateral or lateral and slightly dorsal direction and, antero-medially to the posterior opening of the canal for the v. capitis lateralis *(vcl),* gives off a posterior branch (pls. 31:4-6; 32:1, *IXlp).* This on the left side soon pierces the ventral wall of the endocranium, but is continued by a distinct groove in the ventral side running in lateral and slightly posterior direction immediately anteriorly to the opening of the canal *vcl* (pls. 31:4; 32:1). The main canal *(IXla)* could be followed on the left side only for a short distance in lateral direction before it opens by a foramen in the median side of a large pit in the ventral wall of the endocranium. This pit is probably an anomaly as it is lacking on the right side of the same specimen and is not found in any other species. On the right side of the shield both canals are enclosed in the endoskeleton, and could there be traced somewhat farther distally than on the left side; they lie immediately behind the distal part of the canal *as* and diverge in their lateral course only slightly from each other. They reach most certainly the dorso-lateral outer face of the endoskeleton, but this could not be actually observed. The main branch of the canal *IX* (IX_1) runs in lateral and somewhat ventral and anterior direction, lying close to the posterior and postero-lateral parts of the vestibulum (fig. 11A; pls. 31:6; 32:1) but nowhere has any communication with this cavity been observed. The canal is, however, on the left side very closely associated with the canal *acom,* lying in some places immediately up to this canal, and it has also been observed that the partition between the two canals has disappeared (pl. 31:6). On the right side, the canal IX_1, at least partly and posteriorly, lies at some distance

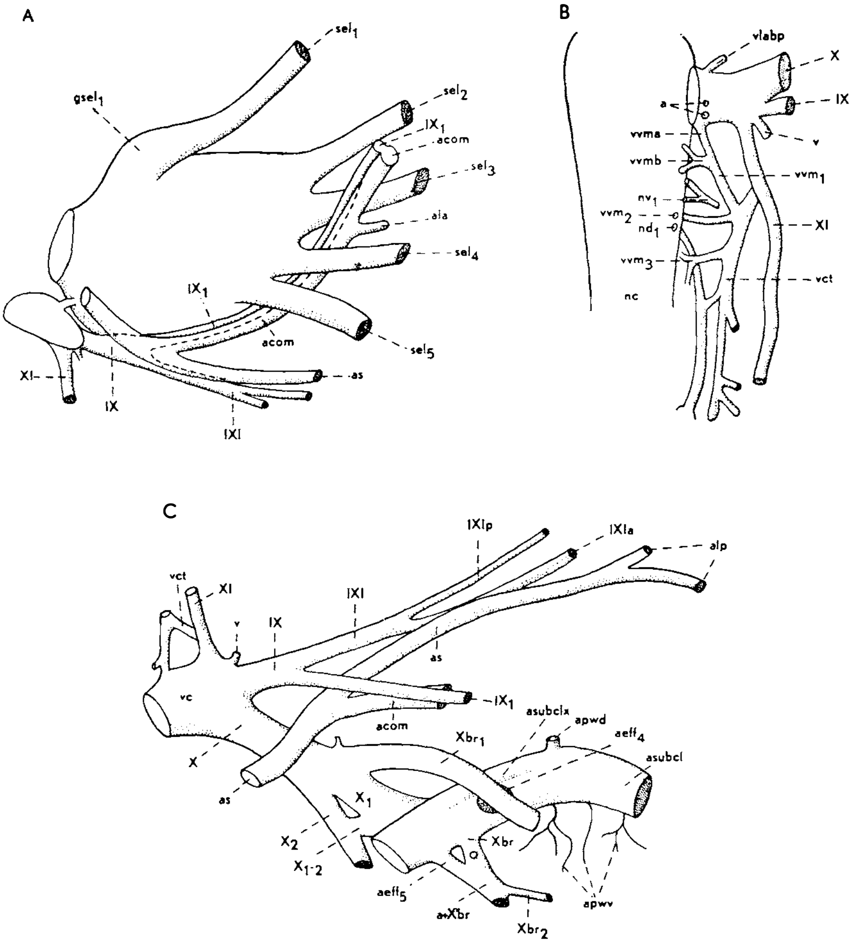

Fig. 11. — *Cephalaspis signata* n. sp. Sketches showing, A, the canals for the n. glossopharyngeus and the a. communicans in relation to the labyrinth cavity and the nerve canals for the lateral sensory field, ventral view; B, the vagus canal with its branches, the canal for the occipital segmental artery and part of the canal for the a. subclavia, seen obliquely from in front; C, the vagus canal and some small canals behind it connected with the neural canal or with the occipital vein sinus, ventral view (the posterior parts of the canals *nd*$_1$ and *vct* are displayed beside each other but in reality the canal *nd*$_1$ lies directly dorsally to the canal *vct*).

a, canals most probably for small arteries to the metotic ganglion complex; *acom,* canal for the a. communicans; *aeff*$_4$, *aeff*$_5$, canals for the fourth and the fifth efferent branchial arteries; *ala,* canal for the common basal trunk of anterior dorso-lateral superficial arteries; *alp,* basal parts of the canals for the posterior dorso-lateral superficial arteries; *apwd, apwv,* canals for arteries to the posterior side of the postbranchial wall; *as,* canal for the a. segmentalis lateralis occipitalis; *asubcl,* canal for the a. subclavia; *asubclx,* groove in the canal for the a. subclavia, of unknown significance; *a* + *Xbr,* common canal for the fifth efferent branchial artery and some branchial rami of the n. vagus; *gsel*$_1$, basal swelling of the canal *sel*$_1$ for a ganglion; *nc,* neural canal; *nd*$_1$, canal for the dorsal root of the first spinal nerve; *nv*$_1$, canal for the ventral roots of the first spinal nerve; *sel*$_1$—*sel*$_5$, canals for the first to fifth nerves of the lateral sensory field;

v, canal for a vein to the occipital vein sinus; *vc,* vagus canal; *vct,* canal for a longitudinal vein to the occipital vein sinus, being i. a. a collector vein for the anterior vertebro-medullar veins; *vest,* vestibulum; *vlabp,* canal for the v. posterior labyrinthi; *vvma, vvmb,* canals for branches of the first vertebro-medullar vein; vvm_1—vvm_3, canals for the first to third vertebro-medullar veins; *IX,* canal for the n. glossopharyngeus; IX_1, canal for the main branch of the n. glossopharyngeus; *IXl,* canal for the r. lateralis glossopharyngei; *IXla, IXlp,* canals for an anterior and a posterior branch of the r. lateralis glossopharyngei; *X,* canal for the n. vagus; X_1, X_2, canals for branches of the n. vagus; $X_{1\text{-}2}$, connecting canal between the canals X_1 and X_2; *Xbr,* canal for some branchial rami of the n. vagus; Xbr_1—Xbr_2, canals for the first and second branchial rami of the n. vagus; *Xl,* canal for the main r. lateralis vagi.

dorsally to the canal *acom* (pl. 30:3). The canal IX_1 accompanies the canal *acom* in its entire course, and lies antero-dorsally or (further distally on the left side) antero-medially, or (on the right side) medially to this canal (pl. 32:2). Distally the canal follows the postero-lateral and lateral sides of the vestibulum. It runs in antero-dorso-lateral direction dorsally to the proximal parts of the canals sel_5 and sel_4 but between the canals sel_4 and sel_3 turns somewhat in antero-ventro-lateral direction and crosses the latter canal on the ventral side (pl. 32:1). On the left side two very narrow canals (pl. 32:1, *n)* are observed; the posterior one of them could be followed down to its exit from the canal *acom* and distally almost to the outer face of the endoskeleton postero-laterally to the orbit.

On the right side of the shield the canal IX_1 opens together with the canal *acom* through a large common opening into the oralo-branchial chamber at the 3rd interbranchial ridge (pls. 29:2; 32:3) lying between (but ventrally to) the canals sel_2 and sel_3. On the left side the terminal point of the main canal IX_1 could not be observed but it is, nevertheless, evident that at least three of its distal branches pierce the roof of the oralo-branchial chamber through openings of their own (pls. 29:2; 31:1-2, IX_1).

The canal *IX* transmitted the n. glossopharyngeus (Stensiö 1927, pp. 53, 69, 71, 87, 191—192). The canals *IXla* and *IXlp* are considered here to have given passage to branches of the n. lateralis posterior, which thus left the vagus canal together with the n. glossopharyngeus, and which thus may be comprised under the name (main) r. lateralis glossopharyngei (main r. lateralis IX). It is, however, very probable that the canals *IXla* and *IXlp* also transmitted general cutaneous fibres, as such fibres enter into the n. glossopharyngeus in *Petromyzon* (Johnston 1905a, p. 186; pl. 5) and also in some Elasmobranchs (Cole 1896, p. 665; Hawkes 1906, p. 978; Kappers 1914, pp. 102—103; cf. Goodrich 1930, pp. 753—754, also Norris & Hughes 1920, pp. 357, 367—368; Daniel 1922, p. 254; Norris 1924, p. 217) and in some Actinopterygians (Johnston 1898, p. 595; 1901, p. 76; Allis 1922, p. 285; Norris 1924, pp. 216—217; 1925, p. 384).

The main stem of the glossopharyngeal nerve went through the canal IX_1, and it very probably consisted of visceral motor and visceral sensory fibres, and probably also contained somatic sensory or possibly lateralis elements. The canals *n*, mentioned above, must, to judge from their straight unbranched course, be assumed to have transmitted nerve-fibres and they must then have traversed the canal *acom* and run on to the glossopharyngeal nerve in the canal IX_1 medially to it.

The largest and topographically most ventral of the branches which leave the vagus canal is the canal for the n. vagus or the vagus canal proper (fig. 11B—C; pls. 30:3; 31:1-5; 32:2, *X;* cf. Stensiö 1927, pp. 53—53). It runs in ventral and somewhat anterior and lateral direction and passes the transverse canal *as* with which it is in open communication (pl. 31:3, 5). Soon afterwards it divides into three main canals.

One of these (Xbr_1) issues from the lateral side of the main canal and travels first in ventro-lateral direction close of the posterior face of the postbranchial wall, and then also in anterior direction and crosses the canal *asubcl* on the dorsal side. It opens into the oralo-branchial chamber close to the interbranchial ridge 4, immediately laterally to the postero-ventral part of the otical prominence caused by the labyrinth cavity, (and thus about normally as in the Cephalaspids, cf. Stensiö 1927, pp. 54, 163, 190; figs. 4, 13, 33, 36; pl. 28). The canal transmitted the first branchial ramus of the n. vagus. Close to the base of the canal Xbr_1 there issues from it a small branch of unknown significance running for a short distance in postero-lateral direction (pl. 31:4, 5).

The canal (X_1) following medially on the canal Xbr_1 is a large one; it could be traced but for a rather short distance in antero-ventro-lateral direction or as far as to the postero-dorsal side of the canal *asubcl.* Its distal branches are not preserved, and the significance of the canal could not be made out beyond that it must have transmitted some of the branchial vagus branches. On its medial side the canal is in open communication by a very short canal ($X_{1\text{-}2}$) with the canal X_2, and opens on its lateral side into the canal *asubcl.*

The most medially disposed branch (X_2) of the canal X is narrower the canal X_1. It runs in antero-ventral and slightly lateral direction and is preserved distally no farther than be canal X_1; as mentioned above, it sends out a very short branch ($X_{1\text{-}2}$) to this canal.

In this connection we must also shortly consider the canal *asubcl* (for the a. subclavia). On the left side of the specimen before us it is only partly preserved, the distal and proximal parts being missing (fig. 11B; pls. 30:3; 31:2-6). It sends out small branches in antero-ventral direction *(apwv)*. One branch *(apwd)* is also observed which, issuing from the postero-dorsal side of the canal, breaks through the posterior face of the postbranchial wall and is continued by a groove on the posterior side of this wall. These small canals contained arteries to the posterior face of the postbranchial wall (cf. Stensiö 1927, p. 183). On the ventral side of the proximal part of the canal *asubcl* there are observed two openings (in pl. 31:4-5, $aeff_5$ and *Xbr).* These are the openings of two extremely short canals, which join to form a short common canal $(a + Xbr$, pl. 31:3). From the antero-lateral part of the common canal near its origin issues a small canal *(x,* only the basal part of it is preserved) of unknown significance. The distal part of the common canal also gives off a branch (Xbr_2) in antero-ventro-lateral direction.

With regard to the question as to what structures were transmitted in these canals, mentioned above, we can say that the canals X_1 and X_2 gave passage to branches of the n. vagus, and the canal X_2 probably to a branch (or branches) for the most median and posterior gill-sacs. As to the significance of the short transverse canal $X_{1\text{-}2}$ I have no definite opinion. The canal $aeff_5$ and a median part of the canal $a + Xbr$ transmitted the a. branchialis efferens 5; the canal *Xbr* and a lateral part of the canal $a + Xbr$ gave passage to the rr. branchiales 2 and 3 (and possibly also to the fourth one) of the n. vagus (and of these the r. branchialis 2 went through the canal Xbr_2 (see further p. 151). Through one of the canals X_1 or X_2 went possibly also a r. intestinalis vagi, if such a branch really was developed in the Cephalaspids (cf. the conditions in recent Cyclostomes, Worthington 1906, p. 174; Cords 1929, p. 238).

Still another canal and its branches in this complex is to be described. In the lateral and ventro-lateral walls of the aortal canal, somewhat before a transverse level through the exit of the vagus canal from the cavum cerebrale, three foramina are seen on the left side (pls. 30:3; 31:2; somewhat more backwards at a level with the origin of the canal nv_1 there is another opening in the lateral wall of the aortal groove leading into a short canal which very soon breaks through the roof of the trunk cavity). The ventro-lateral openings are the openings of very short canals, the posterior one of which runs in postero-ventral direction, and the anterior one in ventral and very slightly posterior direction. Distally they both open in the trunk cavity on the ventral side of the transitional part between the postbranchial wall and the occipital region of the endocranium. The canals must have been traversed by arteries, but nothing definite can be said about their destination or significance; one of them possibly transmitted an artery for the pronephros (cf. *Petromyzon,* Julin 1887, p. 789; pls. 21:6; 22:2; Hatta 1922, p. 151; in *C. hoeli,* however, this artery issued from the a. efferens communis, cf. Stensiö 1927, figs. 35, 39, *a. prn).*

The opening through the lateral wall of the aortal canal (which is observed both on the right and on the left side) leads into a fairly wide canal *(as,* fig. 11B; pls. 30:3; 31:1-2, 4; 32:2). At first this canal runs in lateral and somewhat dorsal direction and immediately anteriorly to the canal *X*, with which it is in open communication, as mentioned above. After having crossed this canal, it soon gives off a branch *(acom)*, which runs in lateral and slightly anterior direction. This canal branch takes a position close to the canal IX_1 and follows it rather intimately (at least on the left side of the shield), as said above. It thus runs in antero-lateral direction close to the posterior and postero-lateral wall of the labyrinth cavity (vestibulum), and during its course gives off small branches to this wall; it passes furthermore dorsally to the basalmost parts of the canals sel_5 and sel_4, turns then somewhat ventrally between the canals sel_4 and sel_3 and runs ventrally to the canal sel_3 (pl. 32:1).

In the anterior part of its course the canal *acom* is seen to give off a branch *(ala*, fig. 11A; pl. 32:1) in dorsal direction, closely behind the canal sel_3. This branch could be traced in dorso-lateral direction almost to the dorsal face of the endoskeleton, postero-laterally to the orbit. It certainly reached this face and gave rise to the canals ala_1 and ala_2 (pl. 29:1), but the actual connection between the basal trunk *ala* and these canals could not be observed (on account of an imperfect preservation of this part of the shield). Whether or not there are other dorsal branches from the canal *acom* which reach the outer face of the endoskeleton could not be ascertained (possibly the canals ala_3 and ala_4 also arose from the canal *ala)*. In the dorsal wall of the canal a small opening is seen (pl. 32:1, *a)*, but where it leads in unknown. Both posteriorly and postero-laterally to the vestibulum the canal *acom*, however, gives off minute branches to the wall of the vestibulum (pls. 30:3; 31:6; 32:1, *avest)*, as said above.

The canal *acom* opens on the right side through a large foramen, common to this canal and the canal IX_1 (pl. 32:2, $IX+acom$), as described above.

Returning now to the main canal *as*, we find that it runs mainly in lateral direction but also somewhat dorsally and slightly posteriorly (fig. 11B; pls. 30:3; 31:1-2, 4-6). On the left side of the shield the canal opens into the above-mentioned pit anterior to the posterior opening of the canal *vcl* (pl. 31:4-6) but laterally to this pit another canal continues in lateral direction. This latter canal *(*as_1, pls. 31:4; 32:1) could be traced rather far laterally and near the outer face of the endoskeleton is seen to divide into two branches which open on this face, one slightly lateral to the other (pls. 29:1, *alp)*. On the right side of the shield the canal *as* remains a closed canal as far as it could be traced, but its distal part is not preserved. Thus it could not be followed on the dorsal face of the endoskeleton (pl. 31:1-2).

If we now consider the question as to the nature of these canals *(as, acom)* and then take into account the origin of the canal *as* and the distal termination of the canal *acom,* as well as their branches on the outer face of the endoskeleton (which will be further dealt with in the chapter on the visceral endoskeleton, p. 118), it is fully evident that the canals in question must have transmitted arteries. The artery in the canal *as* most probably corresponded to a segmental artery in the trunk region in fishes or, more specifically, to an a. segmentalis lateralis (parietal artery, intercostal artery, cf. Daniel 1922, fig. 172; Coles 1928, pp. 98, 102; Corrington 1930, p. 201; Grodzinski 1938, pp. 50—52; Górkiewicz 1947, pp. 247—250; etc), and on account of its proximal course in the occipital region of the endocranium, will be referred to as the a. segmentalis (lateralis) occipitalis (the occipital segmental artery). To judge from the conditions found in *C. doryphorus* (see below), this is the lateral branch of a segmental artery of which the a. encephalica posterior probably is the dorsal branch. Distally the occipital segmental artery gave rise to posterior dorso-lateral superficial arteries, running towards the shoulder-girdle. Through the canal *acom* passed an artery, which created an anastomosis between the segmental artery, just mentioned, and the third a. branchialis efferens, which ran in the groove on the third inter-branchial ridge. The artery is here simply referred to as the a. communicans (and the canal is called the canal for the a. communicans). From the artery originated the anterior dorso-lateral superficial arteries (by means of one or two basal trunks) and furthermore i. a. some small arteries for the vestibular division of the labyrinth cavity, here called the aa. vestibulares.

Looking in the recent Cyclostomes and fishes for structures similar to this a. communicans and its branches, we find that in the Cyclostomes nothing comparable is described, but in fishes we find that dorsal nutrient branchial arteries are commonly given off from the efferent branchial arteries, but that these arteries generally supply deeper structures in the neighbourhood of the gills. Very seldom (in *Lamna,* Burne 1923, p. 227) one of them is developed as a subcutaneous vessel or (as in *Squatina,* Marples 1936b, p. 820; fig. 3) supplies among other structures also the postero-dorsal part of the head. In *Galeus* (Corrington 1930, pp. 203—204, fig. 18) there is formed, by means of the dorsal lateral artery, an anastomosis between the fourth efferent branchial artery and the a. subclavia (which is commonly regarded as a transformed lateral segmental artery). In *Chlamydoselachus* (Allis 1911, pp. 515, 518; fig. 1; 1912, pp. 483—484; 1923, p. 205; fig. 52) a small vessel, considered to be a segmental (vertebral) artery connects the efferent hyal artery with the dorsal aorta; a small branch from this vessel runs along the glossopharyngeal nerve towards the endocranium. This last-named fish thus offers conditions which in some way remind of those in the *Cephalaspis* here treated.

In the other Cephalaspids in the present material in general only small parts of the vagus canal complex and associated canals are exposed. The proximal part of the vagus canal is seen from the median side in an unnamed *Cephalaspis* species (pl. 57:3, *vc)* and, as mentioned above, the corresponding canal (pl. 57:2, *IX + X)* on the right side enclosed only the nn. glossopharyngeus and vagus as well as the associated n. lateralis posterior (or more exactly their roots and ganglia) while the posterior cerebral vein left the cavum cerebrale in a canal of its own (pl. 57:2, *vcp).* The vagus canal *(vc)* is furthermore exposed in cross-section in *C. oreas* (pl. 8:2), *C. excellens* (pls. 14; 15:1; 16—17), *C. doryphorus* (pl. 39:1), and in ventral view in *Nectaspis areolata* (fig. 12; pl. 112:1). In this latter species there is developed a rather long and fairly narrow basal part *(rIX + X)* of the vagus canal while the distal part of the canal is much widened. The basal part must have transmitted i. a. the roots of the metotic ganglia, and these ganglia must have been situated in the distal enlarged part of the canal; the metotic ganglion complex lay thus in *Nectaspis* rather far from the cavum cerebrale (contrary to what was the case in *C. signata).*

The canal *Xl* or its posterior opening in the antero-ventral wall of the inter-zonal endoskeleton is observed in *C. oreas* (pl. 8:2), *C. excellens* (pls. 13—15:1-2; 17), and *C. doryphorus* (pl. 39:1, 3); it will be further considered below (p. 115).

Parts of the canal *X* or its branches *Xbr* and of the canals *IX* and *IXl* are exposed in *C. oreas, C. excellens* and *C. doryphorus* (pls. 8:2: 14; 15:1; 16; 39:1, 3) and *Nectaspis areolata* (fig. 12; pl. 112:1). It will be observed that the canal *IX* (or more exactly the branch corresponding to the canal IX_1 in *C. signata,* treated above) in *C. excellens* and, most certainly also in *C. oreas,* enters the posterior part of the vestibulum, as is evidently normal in the Cephalaspids (cf. Stensiö 1927, pp. 53, 191, etc.); in *Nectaspis,* however, the canal behaves as in *C. signata,* and thus runs behind the vestibulum. It is evidently a composite canal, having enclosed both the n. glossopharyngeus (main branch) and the a. communicans.

In *C. doryphorus* an opening on the right side of the roof of the trunk cavity antero-medially to the posterior opening of the canal *vcl* and laterally to the ridge on the lateral side of the aortal groove represents the termination of the canal *IXl* (pl. 39:1). A short and hardly noticeable groove leads from the opening in lateral direction. Further distally, ventro-laterally to the posterior opening of the canal *vcl* two very narrow grooves are observed, the anterior groove *(IXla,* pl. 39:1) running in ventro-lateral and slightly posterior direction, the posterior one *(IXlp)* in postero-ventro-lateral direction; both grooves open into canals in the endoskeleton at the transition between the inter-zonal and zonal endoskeleton. These grooves and canals probably lodged branches of the posterior lateralis nerve associated with the n. glossopharyngeus, which supplied neuromasts in the lateral part of the supratemporal and the scapular sensory lines.

In the holotype of *C. excellens* the canal *IXl* on the right side opens into the canal *vcl* near its posterior opening (pl. 15:1). Laterally and slightly ventrally and posteriorly to this opening we find a minute opening in the roof of the trunk cavity, which leads into a narrow canal running in lateral and somewhat posterior direction to the outer part of the zonal endoskeleton, in giving off an anterior branch (pl. 14, *n*). On the left side of the same specimen two short grooves on the ventral side of the endoskeleton are seen, which very soon turn laterally and continue as narrow canals. The grooves lie antero-laterally to the posterior opening of the canal *vcl* (pl. 13, *n;* cf. *C. signata);* proximally they pass over into canals (pl. 14, *n)* which certainly join the canal *vcl* slightly before its posterior opening. The canals and grooves *n* have with certainty given passage to lateralis nerves, being branches of the nerve in the canal *IXl*.

In *C. doryphorus* the canal *X* pierces the ventral wall of the endocranium and opens behind the postbranchial wall (pl. 39:3, X_a); the vagus nerve in this canal then went ventro-laterally in a groove (*X*) in the posterior side of the postbranchial wall and finally pierced this wall through the opening X_b in order to reach the gill sacs.

In a specimen of *C. excellens* we find a groove in the most postero-median part of the roof of the oralo-branchial chamber immediately anterior to the postbranchial wall. This groove is seen to run from the aorta groove in lateral and finally also in posterior direction on to an opening (*as*) in the roof (pl. 16:1); this opening in its turn leads into a canal which in pl. 15:1 (*as*) is seen entering the labyrinth cavity associated with the canal *IX*. In the same specimen there is on the right side a groove in the roof of the trunk cavity immediately behind the postbranchial wall and anteriorly to the posterior opening of the canal *vcl,* running in postero-ventro-lateral direction to an opening in the roof at the transition between the inter-zonal and the zonal endoskeleton (pls. 13—14, *asb).* This groove could easily be mistaken for the groove of the occipital segmental artery. It is, however, to be noticed that the groove runs in a postero-ventro-lateral direction towards the zonal endoskeleton and thus lies rather far backwards on the shield. Somewhat postero-laterally to the opening, just referred to, we find the canals asc_1 and asc_2 (for the scapular arteries, see p. 171) entering the dorsal face of the endoskeleton. It seems certain that the arteries in these canals originated from the artery which ran in the groove or canal *asb* (but the actual connection between the groove or canal *asb* and the canals asc_1 and asc_2 could not be observed). The artery thus gave rise to quite other superficial arteries than the occipital segmental artery

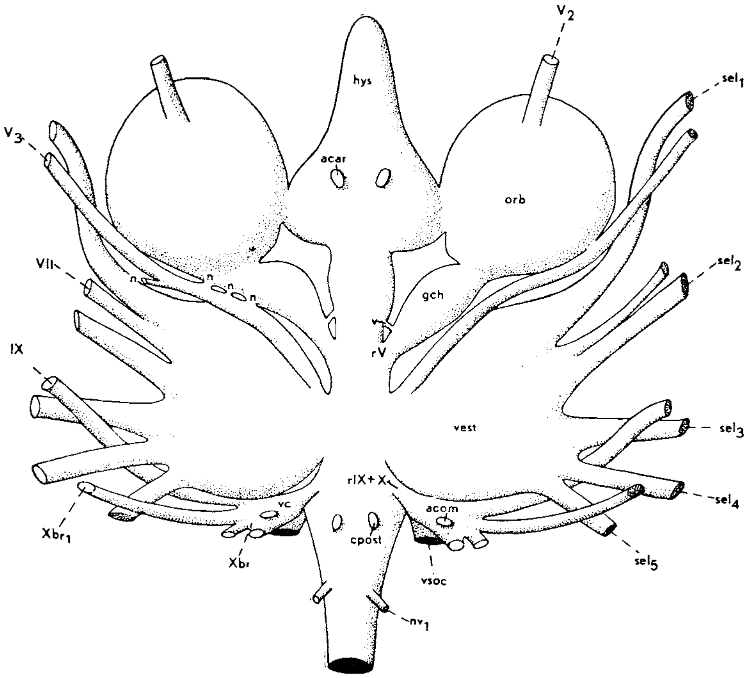

Fig. 12. — *Nectaspis areolata.* Cast of the cavities of the endocranium and the principal nerve canals from them. Restoration mainly after the specimen figured in pl. 112:1. Ventral view. About × 10.

acar, canal for the a. carotis; *acom,* opening into the vagus canal for the a. communicans; *cpost,* canal for the a. encephalica posterior; *gch,* trigeminus-lateralis chamber; *hys,* division of the ethmoidal cavity for the hypophyseal sac; *n,* canals for general cutaneous and/or lateralis fibres from the trigeminus-lateralis ganglion complex, associated with the r. mandibularis V; nv_1, canal for the ventral root of the first spinal nerve; *orb,* orbit; *rV,* canal for the roots of the r. maxillaris V, n. profundus and n. lateralis anterior; $rIX + X$, canal i. a. for the roots of the metotic cranial nerves; sel_1—sel_5, canals for the nerves to the lateral sensory fields; *v,* canal for a vessel; *vest,* vestibulum; *vc,* vagus canal; *vsoc,* occipital vein sinus; V_2, canal for the r. maxillaris V; V_3, canal for the r. mandibularis V; *VII,* canal for the n. facialis; *IX,* canal for the main branch of the n. glossopharyngeus (and probably also for the a. communicans); *Xbr,* canals for some posterior branchial rami of the n. vagus; Xbr_1, canal for the first branchial ramus of the n. vagus.

in *C. signata,* and it seems very probable that the groove *asb* lodged a segmental artery behind the occipital segmental artery. The true occipital segmental artery most probably passed through the canal *as* into the vestibulum.

In the same specimen of *C. excellens* a fairly narrow canal issues from the vestibulum between the basal parts of the canals sel_2 and sel_3 (pls. 14; 15:1; 16:1, *IX)* and, to judge from its size, this canal presumably transmitted only the n. glossopharyngeus. A foramen in the lateral wall of the vestibulum postero-ventrally to the exit of the canal *sel*$_4$ can be interpreted as the possible exit for the a. communicans, but as the canal could not be traced distally, this interpretation is uncertain.

The occipital segmental artery on the right side in *C. doryphorus* possibly left the aorta behind the postbranchial wall and was lodged in a groove in the roof of the trunk cavity in the posterior part of the occipital region at the transition to the postbranchial wall (pl. 39:3, *as?);* the groove ends at an opening (pl. 39:1, *as?)* just laterally to the ridge, bordering the aorta groove on the lateral side. The foramen *as?* leads into a canal which possibly lodged the occipital segmental artery, running to the vestibulum as in *C. excellens.* Laterally and slightly ventrally and posterior to this opening is a long faintly marked groove and, anteriorly to this groove there is seen an opening *(asb?;* pl. 39:1). The groove possibly lodged a posterior branch of a segmental artery, corresponding to that in the canal *asb* in *C. excellens* and the opening *asb?* perhaps transmitted an anterior branch of the same artery. On the left side of the same specimen the canal *as* (for the occipital segmental artery) branches off from the canal *cpost* (pl. 39:4), as related above. It could not be traced for any distance in lateral direction as the shield in this place is imperfectly preserved. Somewhat laterally to the canal *cpost* and antero-medially to the posterior opening of the canal *vcl* there is a low and broad opening in the roof of the trunk cavity, followed in lateral direction by a distinct groove in the ventral side of this lateral part of the occipital region (pl. 39:3, *asb?).* This grove possibly lodged a segmental artery corresponding to the artery in the canal *asb* in *C. excellens.*

In *Nectaspis areolata* only short fragments of the proximal parts of the canal *as* are exposed (pl. 112:1). The canal *acom* (or this is possibly the equivalent to the canal *as)* joins the vagus canal, and the a. communicans was farther distally probably enclosed in a common canal together with the main branch of the n. glossopharyngeus *(IX;* cf. also fig. 12).

We shall now briefly consider the conditions with regard to the vagus canal complex and associated structures in a few *Cephalaspis* specimens previously described, and shall begin with the best preserved specimen studied by Stensiö *(Cephalaspis* sp., used for the series B of sections, Stensiö 1927, pp. 53—56; fig. 14; pl. 85). With the conditions in *C. signata* in mind, we can re-interpret those in that *Cephalaspis* sp. in the following way: the metotic ganglion complex was situated in the vagus canal and not in the fossa *"Xgn"*, the vagus nerve issued through the foramen *"X"*, traversed the mentioned fossa and split into three branches, which entered the openings *"Xbr*$_2$—*Xbr*$_6$*";* the groove *"n. lg."* possibly lodged the a. subclavia; the lateralis fibres, corresponding to those transmitted in the canal *Xl* in *C. signata,* issued through the opening *"IX";* the occipital segmental artery, after having left the aorta, ran in the dorsal part of the fossa *"Xgn"* and in dorso-lateral direction in a groove together with the lateralis fibres just mentioned; the canal *"IXl"* transmitted the main glossopharyngeal nerve, and the canal *"Xl"* the a. communicans; (the opening *"IXp"* in fig. 14 is problematic, cf. pl. 85).

In the wax-models made after the series A of sections, and figured by Stensiö (1927, figs. 18, 24; Holmgren & Stensiö 1936, fig. 217) the canal *"IXa"* is seen to be strikingly wide; it had transmitted not only the n. glossopharyngeus (the main branch) but also the a. communicans.

In an undeterminable *Cephalaspis* specimen, figured by Stensiö (1927, pl. 28) the canal *"IXa"* is probably the canal for the a. communicans and the canal *"IXav"* probably transmitted a nutrient artery to the roof of the oralo-branchial chamber (cf. *C. kozlowskii* below); an unlettered canal, seen medially to this canal, is probably the canal for the (main) n. glossopharyngeus.

In *C. kozlowskii* Zych (1937, pp. 69—72, cf. p. 91; pls. 2, 4:1) has described interesting conditions with regard to dorso-lateral superficial arterial canals and their proximal connections, and I can here, after having examined his material, make some additional notes. The canals for the anterior dorso-lateral superficial arteries join proximally forming a common trunk *("a. la"* or *"a. lc + IX")* which in its turn opens into a canal *("a. scom")* behind the labyrinth cavity. The canal *"a. scom"* is said to issue from the aorta groove, but the actual connection between them is not seen as the shield is imperfectly preserved in this place. Nevertheless, the canal *"a. scom"* corresponds to the canal *as* (in the present paper), and it must thus really have issued from the aortal groove (or canal). The posterior part of the canal *"a. la"* (or *"a. lc + IX")* corresponds to the canal *acom* (in *C. signata* and others). The main anterior continuation of the canal was not observed by Zych; on further preparation of the specimen, described by him, it was, however, found to run down through the endoskeleton and to open in the oralo-branchial chamber as in *C. signata*. It can be noticed that the canal in the main passes behind the labyrinth cavity but that it is for a short distance in open communication with the vestibulum at the postero-lateral corner of the cavity. Somewhat behind its opening into the oralo-branchial chamber the canal gives off from its ventral side a narrow canal to the roof of the said chamber (this canal is interpreted as having transmitted a nutrient artery). In the lateral wall of the vestibulum, just dorsally to the exit of the canal sel_4 ("sel_5", Zych) there is an opening leading into a very short canal joining the distal part of the canal *acom*. This is the canal for the (main) n. glossopharyngeus. The distal part of the canal called *acom* is thus, at least partly (the anterior side of the canal was not exposed and it is thus uncertain whether the canal farther distally bifurcates or not), a composite canal, transmitting both the a. communicans and the n. glossopharyngeus. It is evident that this latter nerve must have traversed in this species at least a small part of the labyrinth cavity, but it could not be ascertained whether in proximal direction it ran through the proximal part of the canal *acom* and the canal *as* (and it was by Zych assumed to have done so and to have lain entirely behind the labyrinth cavity) or independently through the labyrinth cavity and pierced its posterior wall by an opening of its own. The distal part or lateral continuation of the canal *as ("a. scom")* is imperfectly preserved; it soon branches into two canals. Both of them are without doubt arterial canals (and the anterior one certainly did not transmit a branch of the n. vagus as supposed by Zych 1937, p. 70). Indubitably the canals served the passage of posterior dorso-lateral superficial arteries.

The inter-zonal endoskeleton.

For the sake of convenience the inter-zonal endoskeleton will be described here, after the account of the occipital region of the endocranium, although it does not belong to the head division of the cephalic shield (and its description would most logically follow after that of the visceral endoskeleton). It will furthermore be treated as an entirety and, thus, the inter-zonal axial endoskeleton and the dorsal inter-zonal endoskeleton are not described separately.

The ventral face of the inter-zonal endoskeleton is provided with a generally well developed neural ridge (cf. Stensiö 1927, pp. 48, 50), which encloses the canal for the spinal cord (the neural canal); anteriorly the ridge passes over into the rapidly widening posterior part of the occipital region. It forms part of the axial endoskeleton. As noted by Stensiö (1927, p. 50) it does not usually reach backwards as far as to the posterior end of the inter-zonal part, and its dorsal part generally extends farther posteriorly than its ventral part in such a way that the posterior opening of the neural canal has a more or less oblique position.

In *Boreaspis,* however, in which genus it is strongly developed, the neural ridge *(nr)* reaches as far backwards as to the posterior end of the inter-zonal part. Here it is abruptly truncated so that the opening of the neural canal *(nc)* faces straight backwards (pls. 79:1; 82:3; 91:1; 92:5). Also in some *Cephalaspis* species the neural ridge reaches equally far backwards or nearly so *(C. hoeli, C. retusa,* pls. 9:7; 10:2) but generally it ends before that point *(C. excellens, C. oreas, C. doryphorus,* etc., pls. 8:2; 13; 16:2; 39:1; 56:2). In some species, best seen in *C. hastata?* (pl. 32:4), the axial endoskeleton in the posterior portion of the inter-zonal part only formed a roof over the spinal cord or, in other words, the spinal cord was partly lodged in a groove on the ventral side of the inter-zonal endoskeleton; this is an extreme case of the condition, referred to above, that the dorsal part of the neural ridge extends further backwards than the ventral one. The groove, just mentioned, will be called the neural groove.

The groove on the ventral side of the neural ridge for the notochord (cf. Stensiö 1927, pp. 50—51) is seen in pl. 8:2, and in its most anterior part, in pls. 17 and 39:1.

On the ventral side of the inter-zonal endoskeleton and in its anterior part the broad groove for the aorta dorsalis, if observable, is found on the right side of the neural ridge in *Cephalaspis;* in some cases it is on the lateral side bordered by a sharp-edged ridge (pls. 3:1; 8:2; 13—14; 15:1; 16:2; 17; 32:4; 33:1; 56:1).

In *C. signata* (fig. 11C; pls. 31:4; 32:1) it has been shown above (p. 90) that a small canal *vvma* from the vagus canal joins another small canal *(vvmb)* from the neural canal to form a common canal vvm_1 running in postero-dorso-lateral direction to the canal *vct.* More precisely, the canal *vvmb* has arisen from the union of two minute canals coming from the ventral side of the lateral part of the neural canal just behind the origin of the vagus canal. Just posteriorly to the point of union of the canals vvm_1 and *vct* a small canal vvm_2 issues from the latter canal and runs in medial and slightly posterior direction to the neural canal, where it opens on the lateral side of this canal immediately before the opening of the canal nd_1. The canal *vct* continues in posterior direction, and slightly behind the origin of the canal vvm_2 another small canal (vvm_3) runs from the canal *vct* in ventro-medial and slightly posterior direction turning most medially somewhat in anterior direction and reaching near to the neural canal, but, because of the imperfect preservation, its connection with this canal is not seen; it seems nevertheless very probable that it really joined the neural canal. Just laterally to this canal the canal vvm_3 gives off a canal in posterior direction. Shortly behind the origin of the canal vvm_3 the canal *vct* sends out a connecting canal to the canal nd_1 and, slightly posterior to this point, another small canal in postero-ventro-lateral direction. The canal *vct* runs farther backwards, and is now lying directly ventral to the canal nd_1. It ends at about a transverse level with the foramen d_1 (the posterior part of the dorsal sensory field) in opening into the trunk cavity rather near to the neural ridge; slightly before this point it sends out a couple of small branches in dorso-lateral direction (they could not, however, be traced far distally, and their destination is thus unknown). Just behind the posterior inner opening of the canal *vvmb,* but from the ventro-lateral side of the neural canal, two minute canals issue; they soon unite to form a common canal (nv_1) which runs in ventro-lateral direction (and very probably pierces the roof of the trunk cavity near the neural ridge). Immediately behind the opening into the neural canal of the canal vvm_2

and at the same horizontal level, the canal nd_1 emerges from the neural canal; it runs in posterior direction with a very slight lateral bend, crosses the canal vvm_3 on the dorsal side and receives, slightly behind this point, a small branch from the canal *vct* (as mentioned above). Further distally the canal nd_1, which is now somewhat wider than before, lies dorsally to the canal *vct;* in its posterior course the canal turns dorsally and opens under the posterior part of the dorsal sensory field into a fairly wide sinus-like canal (which is only partly preserved). It may also be mentioned that the anterior part of the neural canal receives from below some small canals, evidently coming from the dorsal part of the aortal groove.

The minute canals *nv* are, besides in *C. signata,* exposed only in a specimen of *C. excellens,* in which two of them (nv_1, nv_2) have been observed (the posterior one of them is seen in pl. 13, nv_2). In *C. oreas* in found a pair of canals possibly representing these canals (pl. 8:2, *nv?).* In *C. excellens* the canals issue from the ventro-lateral side of the neural canal, the anterior one somewhat nearer to the median line than the posterior one; they thus originate in the same way as the canal "nv_1" in a *Cephalaspis* sp. described by Stensiö (1927, p. 57; figs. 16—17, 24; pl. 74; Holmgren & Stensiö 1936, fig. 214; cf. fig. 10, this paper). Slightly behind the canal nv_2 there is found in the same specimen of *C. excellens* another canal (nd_2), also minute but a little larger than the canal nv_2, which issues from the neural canal at a slightly higher level than the canal nv_2 (and thus much as the canal "nv_2" in a *Cephalaspis* sp., figured by Stensiö 1927, figs. 16—17, 24; pl. 73; Holmgren & Stensiö 1936, fig. 214; cf. this paper, fig. 10, nd_1).

At a transverse level with the exit of the canal nv_2 in *C. excellens* the canal *acrl,* mentioned before (p. 89), issues in the median line from the dorsal side of the neural canal (pls. 13; 15:2). This canal could be followed backwards to the posterior end of the endoskeleton, lying below the longitudinal dorsal crest, and it is beyond doubt that the artery which passed in this canal must have continued farther backwards and thus into the tissues of the dorsal crest of the scale-covered division of the trunk. On the right side the canal is seen to give off a small dorso-lateral branch (pl. 15:2, $acrl_1$).

Immediately before or, more exactly, anteriorly and slightly laterally to the origin of the canal *acrl* the proximal opening of another canal is observed (pls. 13; 15:2, vvm_1s). This canal could be followed in postero-dorso-lateral direction and was found to join the posterior part of the occipital vein sinus (in about the same way as the canal "nd_1" in *Cephalaspis* sp. and *Kiaeraspis,* Stensiö 1927, p. 57; figs. 23—24, 26—27; Holmgren & Stensiö 1936, fig. 218). Slightly before the exit of this canal there issues from the right dorso-lateral side of the neural canal another small canal (vvm_1d, pl. 15:2; its point of origin is also seen in pl. 13), which runs in postero-dorso-lateral direction; this canal corresponds to the canal *vvm*$_1$*s* on the left side. At some distance behind these canals there issues a pair of canals from the dorso-lateral side of the neural canal; the origin of the left one lies slightly before that of the right one. The canal on the right side (pls. 14; 15:1, *vvm*$_2$) is observed to run in postero-lateral direction and to open into the trunk cavity near the neural ridge (in pl. 13 only the proximal and distal openings of the canal are seen). Immediately below the exit of this canal another canal issues from the lateral side of the neural canal, runs in postero-lateral direction, lying just ventrally to the canal *vvm*$_2$, and opens below the distal opening of this canal, thus also into the trunk cavity (pl. 13, *nd*). The corresponding canals *vvm*$_2$ and *nd*$_3$ on the left side of the shield have a common proximal and a common distal opening (pl. 15:1, *vvm*$_2$, *nd*$_3$). Farther posteriorly on the right dorso-lateral side of the neural canal the exit of yet another canal is seen (pls. 13; 14, *vvm*$_3$). A couple of the canals *vvm* is also seen in another specimen of *C. excellens* (pls. 16:2; 17).

In *C. doryphorus* (pl. 39:3) a pair of narrow canals *nd* is seen to issue from the lateral part of the neural canal and at about the same transverse level, and somewhat behind them another pair of canals *(vvm)*, which are somewhat wider than the canals *nd*, and which issue from the dorso-lateral side of the neural canal, the right one slightly anteriorly to the left one. Both pairs of canals open into the trunk cavity just laterally to the neural canal (or groove).

The canal *nv*$_1$ in *Cephalaspis* sp. is interpreted by Stensiö (1927, pp. 57—58) as having transmitted the first spinal nerve ("spino-occipital" nerve), and most probably only the ventral (motor) root of this nerve and in addition also a vertebro-medullar ("myelonal") artery. The canal *nv*$_1$ in *C. excellens* and *C. signata* is here considered to be the canal for the ventral root of the first, and the canal *nv*$_2$ in *C. excellens* to be the canal for the ventral root of the second spinal nerve.[1] I find it, however, rather unlikely that the canals should have transmitted also vertebro-medullar arteries, if we take into account the minute size of the canals and the probability that the ventral part of the neural canal was supplied with arteries from the aorta directly, and the dorsal part with arterial branches from the proximal part of the a. spinae dorsalis (or a. cristae dorsalis), and make a comparison with the conditions in *Petromyzon,* in which the arteries for the rhombencephalon and the anterior part of the spinal cord are branches of the posterior cerebral artery (Cori 1906, pl. 1; Sterzi 1907, fig. 70). In *C. signata* the ventral root of the first spinal nerve (in the canal *nv*$_1$, fig. 11) must have issued from the spinal cord by means of at least two rootlets, as the canal *nv*$_1$ arises by

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[1] That they were traversed only by the motor roots is made probable from what is said below with regard to the canals *nd*.

the union of two small proximal canals coming from the neural canal. Also the canal in front *(vvmb)* originates in the same way, but as this canal finally reaches the canal *vct* and does not pierce the roof of the trunk cavity it cannot have been traversed by any ventral (motor) nerve root.

The canals nd_1 in *C. signata* and nd_2 in *C. excellens* are interpreted as having each been traversed by the dorsal root of a spinal nerve, and, to judge from the position behind the canal nv_1 and nv_2 respectively for the ventral root of the first and second spinal nerves, the root in the canal nd_1 must have been the dorsal root of the first, and the root in the canal nd_2 the dorsal root of the second spinal nerve (cf. *Petromyzon,* Freud 1877, pp. 22—24; 1878; pp. 150—152; Johnston 1905a, pl. 5, cf. p. 182; Tretjakoff 1927a, fig. 21; Addens 1933, p. 386; etc., and *Eptatretus,* Worthington 1906, p. 176; Allen 1917, pp. 142—156; Addens 1933, p. 403; etc.). The canal nd_3 is the canal of the dorsal root of the third spinal nerve, and it must be noticed that this nerve-root must have run rather closely associated with the first normally developed vertebro-medullar vein (which is thought to have traversed the canal vvm_3, see below, p. 109).

The canal nd_1 in *C. signata* is, however, as to its origin, quite corresponding to the canal "nv_2" in *Cephalaspis* sp., described by Stensiö (1927, pp. 59—60; figs. 16—17, 24; pl. 73), and the canal nd_2 in *C. excellens* has, with regard to its position, already been compared with this canal. The canal "nv_2" of Stensiö is by him interpreted as having been traversed by the ventral root of a spinal (spino-occipital) nerve and an a. vertebro-medullaris (Stensiö 1927, p. 60).

The canal nd_1 in *C. signata* cannot, by reason of its dorsal position within the inter-zonal endoskeleton, have given passage to a ventral nerve root. That the structure in the canal nd_2 in *C. excellens* was a ventral nerve root and thus serially homologous to that in the canal nv_2 seems very improbable, since the canal nd_2 lies much too closely to the canal nv_2; the distance between the exit of the canals nv_1 and nv_2 in the examined specimen is 1.5 mm and between that of the canals nv_2 and nd_2 only 0.4 mm (between the exit of the canals nd_2 and nd_3 it is 1.3 mm). Although the distance between two subsequent ventral roots in *Petromyzon* is rather variable (cf. Freud 1877, p. 23; Julin 1887, pl. 22:2-4) a comparison with this animal makes it very probable that the canals nv_2 and nd_2 did not transmit serially homologous structures but were traversed by different structures, and thus one by the ventral, the other by the dorsal root of a spinal nerve. It can furthermore be noted that although the dorsal root in *Petromyzon* leaves the spinal cord from the dorsal side it traverses the endorhachis in the lateral or ventro-lateral wall of the neural canal (Freud 1877, fig. 2; Tretjakoff 1927a, fig. 25) but on a higher level than the ventral root (cf. Tretjakoff 1927a, fig. 26).

A canal for the dorsal root of the first spinal nerve has not been observed in *C. excellens,* either because of its not being preserved or else because this dorsal root was lacking in the species; it was present in *C. signata* (in *Petromyzon* the first spinal nerve is said to be represented only by a ventral root, Tretjakoff 1927a, p. 407, but this is not in accordance with the facts brought forward by Addens 1933, pp. 385—386).

The canals vvm_1s and vvm_1d in *C. excellens* form a pair of canals which correspond to the canals "nd_1" in the Cephalaspids, described by Stensiö (1927, pp. 57—58; figs. 15—17, 20—28; pls. 18; 19:1; 73—74; 89; 102—103) and interpreted by him as canals for the first vertebro-medullar ("myelonal") vein and probably also for the dorsal root of the first spinal nerve; this latter assumption is, however, certainly wrong. No dorsal roots leave the neural canal so far dorsally as these canals in *C. excellens* and the position of canals which undoubtedly had been traversed by dorsal roots (nd_3 in this species; nd_1 in *C. signata)* is quite different. I thus consider the canal vvm_1 in *C. excellens* as being the canal for the first vertebro-medullar vein, and as the canal joins the occipital vein sinus the vein must have emptied in this sinus and through it into the v. capitis lateralis; it thus belonged to the system of the anterior cardinal veins. The canal "nd_1" in Stensiö's descriptions must accordingly also have been a canal only for the first vertebro-medullar vein, and I think it highly probable that the dorsal root of the first spinal nerve went through the canal lettered "nv_2" by Stensiö.

In *C. signata* the veins from the posterior part of the medulla oblongata and the anteriormost part of the medulla spinalis joined a longitudinal vein stem (in the canal *vct),* laterally to the neural canal, which emptied into the occipital vein sinus. The anterior part of the vein in the canal *vct* can be compared with the longitudinal collector vein for the anterior dorsal segmental veins, discharging into the v. cerebralis posterior in *Petromyzon* (Cori 1906, pp. 50—51; pl. 1; cf. also Stensiö 1927, fig. 99). The veins in the canals vvm_1, vvm_2, and most probably also in the canal vvm_3, are most naturally regarded as vertebro-medullar veins. As to the nature of the posterior part of the vein in the canal *vct* I have no definite opinion (see below and p. 226). The canal *vct* corresponds probably partly to the canal with the same lettering in *Cephalaspis* sp. and *Kiaeraspis,* described by Stensiö (1927, pp. 62—63; figs. 14, 24, 26; pls. 74—75; 84; 101—102) and interpreted by him as the canal for an anterior segmental vein. It is to be noticed that the vertebro-medullar vein canals in *C. signata* enter the neural canal in its ventral half and thus very low as compared with *C. excellens* and other species.

As the vertebro-medullar vessels represent median branches of dorsal segmental vessels, arising from the dorsal aorta or the cardinal veins, the first vertebro-medullar vein in *C. excellens* and the anterior ones in *C. signata* had an anomalous disposition and were thus transformed vertebro-medullar veins (cf. the conditions in *Petromyzon,* Cori 1906, pp. 50—51, pl. 1; cf. also Hatta 1922, p. 183).

The canal *vvm*$_2$ in *C. excellens* gave passage to the second vertebro-medullar vein, and the canal *vvm*$_3$ to the third one. It is important however, to note that, to judge from the place of the distal openings of the canals, these veins could not have emptied (directly or indirectly) into the occipital vein sinus (contrary to what was the case in the preceding vertebro-medullar vein). If we consider that in the Cephalaspids the heart very probably was situated closely behind the ventral part of the postbranchial wall (Stensiö 1927, p. 204), then it seems probable that the posterior cardinal veins had reached so far anteriorly that they could have received the vertebro-medullar veins behind the first one in *C. excellens,* and the vein in the canal *vvm* in *C. doryphorus.* Possibly also the longitudinal vein in the canal *vct* in *C. signata* opened downwards into the posterior cardinal vein, and thus constituted an anastomosis between this vein and the occipital vein sinus.

Because of the openings in a similar way into the trunk cavity of the canals *"nd"* and *"nd*$_1$*", "nd*$_2$*"* in *C. exilis* and *Hoelaspis angulata* (Stensiö 1927, p. 58; pls. 23:3; 44) the vertebro-medullar veins in these canals also possibly opened into the posterior cardinal veins.

In a specimen of *C. hastata?* (pls. 32:4; 33:1) an aberrant condition with regard to a canal issuing from the neural canal (or groove) is to be noted: besides some canals for dorsal spinal nerve roots *(nd)* and some apparently normally developed canals for vertebro-medullar veins *(vvm),* there is found a pair of canals which issue from the dorsal side of the neural canal (or groove); the right one is preserved only in its most basal part but the left canal *(vnc)* runs in antero-dorsal direction, then bends over to the right side and turns in lateral and slightly postero-ventral direction; it is not preserved farther distally. In the dorsal roof of the aortal groove there is, however, an opening, which in postero-ventro-lateral direction is continued by a narrow groove in this roof. It disappears after a distance. The opening and the narrow groove are disposed in such a way that the structure transmitted in the canal *vnc* probably continued distally in them. As to the nature of this structure I have no definite opinion; possibly it was a transformed vertebro-medullar vein which had an anomalous passage because of the asymmetrical development of the heart or the ductus cuvieri and the veins emptying into it (cf. recent Cyclostomes, Jackson 1901; Cori 1906; Hatta 1922, p. 168; Cole 1925; etc.).

We shall now turn to a consideration of the canals in the posterior part of the inter-zonal endoskeleton, including those of the dorsal spine.

In an unnamed *Cephalaspis* sp. (fig. 13; pl. 56:1-3) a pair of canals *(vvm)* for vertebro-medullar veins leaves the neural canal (or groove) somewhat behind the exit of the arterial canal *adsp*. The right one of these canals was followed in posterior and somewhat dorsal and lateral direction and was found to join the canal for a dorsal segmental vein in the antero-basal part of the dorsal spine (fig. 13). A small opening into the wall of the cavum cerebrale at the transition to the neural canal, seen on the right side (of the same specimen, pl. 57:2, *vvm?)* is possibly the opening of a canal for an anterior vertebro-medullar vein.

In the posterior part of the inter-zonal endoskeleton we find on the ventral side (in the same unnamed *Cephalaspis* sp., fig. 13; pl. 56), two longitudinal series of openings, one on each side of the median line *(asd,*[1] *vsd)*. The three posterior openings lead into ascending canals (which are preserved only in their basal parts and which thus could not be followed far distally); they possibly are all canals for dorsal segmental veins.

The most anterior canal *(vsd_1)* receives (observed on the right side only), as said above, near its base the canal *vvm* coming from in front; the canal vsd_1 runs in dorsal direction and divides into three branches to the most anterior ventral part of the dorsal spine. The canal vsd_1 transmitted a dorsal segmental vein and received through the canal *vvm* a vertebro-medullar branch.

The second vein canal *(vsd_2)* is well developed; it consists of a main stem and an anterior branch; the former splits, as far as observed, into two distal canals which antero-laterally to the dorsal spine reach the outer face of the endoskeleton, and here give origin to two superficial vein canals *(vsds);* the main stem is by a narrow canal connected with the canal *adsp*. The anterior branch runs in anterior and slightly dorsal and medial direction, and as a whole lies near the median line of the shield and thus more medially than the posterior branch. It splits into three distal branches near the branches of the canal vsd_1, and these branches ascend to the superficial area in the median line between the dorsal sensory field and the basis of the dorsal spine. By a very short but fairly wide canal the anterior branch communicates with the canal *adsp*. Slightly behind this point it gives off a dorsal branch which splits into five fairly small dorsal canals *(dspc)* ascending to the anterior part of the dorsal spine, and also a small canal to the posterior main stem of the canal *(vsd_2)*. The anteriorly directed part of the anterior branch certainly transmitted veins but several of the canals of its dorsal branch very probably gave passage to arteries for the dorsal spine, and one of them possibly gave origin to the superficial canal *adsps* on the side of the dorsal spine (pl. 56:3).

The canal *adsp* (corresponding to the canal for the a. spinae dor-

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[1] *ads* in fig. 13.

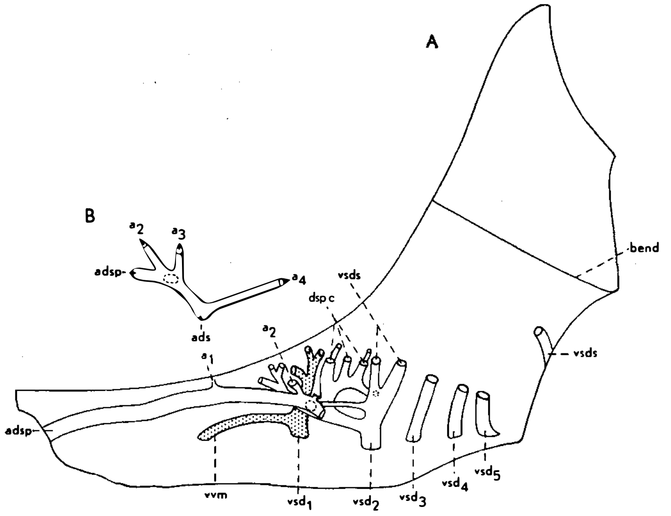

Fig. 13. — *Cephalaspis* sp. (same specimen as in pls. 56—57). A, vascular canals in the basis of the dorsal spine; the canals belong to the left side of the shield with exception of the shaded canals which lie on the right side; lateral view; about × 3. B, postero-lateral continuation of the canal *adsp* (with branches), seen obliquely from in front.

a_1, dorsal branch from the canal *adsp,* enclosing an artery to the dorsal sensory field; a_2—a_4, basal parts of canals for superficial arteries to the dorso-median region of the inter-zonal part at the base of the dorsal spine; *ads,* canal for a dorsal segmental artery; *adsp,* canal for the a. spinae dorsalis; *bend,* dorsal border of the endoskeleton in the dorsal spine; *dspc,* canals to the dorsal spine, at least partly for arteries; *vdsp,* canal for a posterior superficial vein on the side of the dorsal spine; $vsd_{1\text{-}5}$, canals for dorsal segmental veins; *vsds,* basal part of canals for superficial branches of a dorsal segmental vein; *vvm,* canal for a vertebro-medullar vein.

salis in other *Cephalaspis* species), after its origin from the neural canal, runs, as said before, in posterior direction, lying near the median line, but gradually turns somewhat over to the left side; during its course it gives off a short canal (a_1) to the most posterior part of the dorsal sensory field, and farther backwards another canal (a_2) to the outer face of the endoskeleton antero-laterally to the base of the dorsal spine. The canal *adsp* posteriorly divides into two branches. The right one is very short and joins the anterior branch of the canal vsd_2, as mentioned above; the left branch runs in postero-ventral direction and terminates in an opening (*asd*[1]) in the ventral wall of the inter-zonal endoskeleton just anteriorly to the opening of the canal vsd_2. Immediately after its origin the left branch gives off a small canal (a_3), which gives rise to a superficial canal lying just ventro-laterally to the superficial canal a_2 (pl. 56:3), and near to the posterior opening *asd* issues another rather long canal (a_4), running in lateral and slightly dorsal and posterior direction, and also ending in a superficial canal,

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[1] *ads* in fig. 13.

which lies behind the vein canal *vizl* (pl. 56:3, a_4). The canals a_{1-4} transmitted arteries, and, to judge from the disposition of the canals a_{2-4}, the arteries in these three canals were most probably branches of a dorsal segmental artery which entered the endoskeleton through the opening *asd*. The a. spinae dorsalis thus ran in the canal *adsp* backwards to the branching of this canal and then through its right branch; a small branch of the artery may have entered the left branch and passed in the connecting canal between the canals *adsp* and vsd_2.

On the basal part of the dorsal spine a fairly strong vein canal *(vdsp,* pl. 56:3) runs in posterior direction and turns most distally somewhat ventrally before it opens at the posterior margin of the endoskeleton. It most probably transmitted a dorsal segmental vein which thus must have joined the posterior cardinal vein in the trunk division behind the cephalic shield.

In *C. doryphorus* there are two arterial canals for the dorsal spine. The canal for the anterior a. spinae dorsalis *(adspa,* pl. 39:4) enters the foremost part of the dorsal spine; it does not break up into small canals as is evidently the case in the *Cephalaspis* sp., just described. The posterior part of the spine is traversed by a vertical canal which opens on the ventral side of the endoskeleton of the spine, slightly to the right of the median line (fig. 6B; pl. 39:1, 4, *adspp).* This canal is interpreted as the canal for a posterior a. spinae dorsalis. On the left side of the dorsal spine two superficial canals are seen which very probably are arterial canals; one of them *(adspas,* pl. 40:2) is probably a branch of the canal for the a. spinae dorsalis anterior; the posterior one *(adspps,* pl. 40:2) is seen to open into the canal *adspp*. Between these canals there is a superficial canal *(v,* pl. 40:2) which probably gave passage to a branch of a segmental vein.

In an undetermined fragment (probably of a *Cephalaspis* sp.) the vein canals on the lateral side av the dorsal spine are beautifully exposed (pl. 59:2). A number of vertical canals join a common trunk in the basal part of the spine, and this trunk runs in antero-ventral direction but could not be followed far. It is thus uncertain whether it joined the lateral inter-zonal vein canal (see below) or is formed by one or several dorsal segmental vein canals, but the latter supposition seems the most plausible one.

In the dorsal spine of the holotype of *C. hastata* (pl. 35:1) short superficial canals are seen in its basal part; they soon enter deeper parts of the endoskeleton in the spine and thus cannot be traced far. Near the top of the spine there is one pair of vertical canals *(dspv)* on each side, which certainly consists of a vein and an artery canal.

After this fragmentary account of the canals in the dorsal spine we shall now consider some superficial canals in the inter-zonal endoskeleton, which in general do not extend to the dorsal spine.

In the unnamed *Cephalaspis* sp., frequently mentioned above, a well developed longitudinal canal with numerous branches lies on the dorso-lateral side of the shield, laterally to the posterior part of the dorsal sensory field; anteriorly the canal turns ventrally into the endoskeleton and joins the postero-lateral part of the occipital vein sinus (pl. 56:3, *vizl).* This canal will be referred to as the canal for the lateral inter-zonal (superficial) vein. The anterior part of the canal corresponds to the canal *"v. ol"* (for "the lateral occipital vein") in a *Cephalaspis* sp., described by Stensiö (1927, p. 64; figs. 23—26).

In *C. doryphorus* the lateral inter-zonal vein (in the canal *vizl,* pls. 39:4; 40:2) also drained the superficial parts of the anterior region of the basal dorsal spine. To judge from its disposition, the canal *vizl* must have entered the dorso-lateral part of the occipital vein sinus, just as the corresponding canal in the *Cephalaspis* sp. mentioned above.

In a specimen, doubtfully assigned to *C. hastata,* the canal *vizl* is strongly developed (pl. 32:4) as far backwards on the shield as well behind the level of the openings d_1, and the vein in it had possibly contributed to the drainage of the dorsal spine. A longitudinal canal *vizm* lies dorsally and somewhat medially to the canal *vizl* and is found anteriorly to join the canal d_1, which opens into the postero-median part of the occipital vein sinus. The canal *vizm* is thought to have transmitted a vein, which is here called the median inter-zonal (superficial) vein and the canal *vizm* is referred to as the canal for the median inter-zonal vein. The canal is possibly homologous to the canal lettered "nd_1m" by Stensiö in a *Cephalaspis* sp. (Stensiö 1927, figs. 23—24, 26).

In the holotype of *C. hastata* parts of the canals *vizm* and *vizl* are seen (pl. 36:2); they both give off small superficial branches. Thus some small canals *(vizms)* are observed running from the canal *vizm* to the most posterior part of the dorsal sensory field.

In *C. signata* the canal *vizm* is not developed; there is no posterior canal from the postero-median corner of the occipital vein sinus in which the canal d_1 opens. On the shield behind the opening of the canal d_1 and along the base of the dorsal spine there is, however, seen a longitudinal series of five comparatively small superficial canals (vsd_1—vsd_5, pl. 29:1) which from their origin on the outer face of the endoskeleton run in ventro-lateral direction, generally in branching frequently. The first of these canals (vsd_1) does not join a median inter-zonal vein as could have been suspected with regard to its position closely behind the canal d_1; the canal could be traced for a short distance in straight ventral direction (but its basal part is not preserved). To judge from their position and by comparison with the unnamed *Cephalaspis* sp., mentioned above, it seems very probable that all the canals vsd_1—vsd_5 were canals for superficial branches from dorsal segmental veins. A superficial rather feebly developed bifurcated canal *(vizl,* pl. 29:1), corresponding to the canal for the lateral inter-zonal vein in other *Cephalaspis* species, is seen ventro-laterally to the canals vsd_1—vsd_2. It does not enter the dorsal spine. Proximally it was found to join the occipital vein sinus; more precisely, the postero-lateral corner of the occipital vein sinus passes over into a canal which soon divides into a dorsal branch which eventually reaches the outer face of the endoskeleton and gives rise to the superficial canal *vizl,* and a ventral branch which, splitting into two canals, pierces the roof of the trunk cavity, postero-dorso-medially to the posterior opening of the canal *vcl* (pls. 31:4; 32:1, *vsocv).* Some canals in the anterior part of the dorsal spine (pl. 29:1, *adsp?)* are possibly branches of the canal for the a. spinae dorsalis (no other canals are preserved in the dorsal spine of the specimen examined).

In *C. hoeli* (pl. 10:2) the canal for the lateral inter-zonal superficial vein *(vizl)* is well developed as a longitudinal canal with numerous branches, and it is also found developed in a similar way in *C. sinuata* (pl. 23:1) and in an unnamed *Cephalaspis* specimen (pls. 59:1; 60). In the posterior region of the inter-zonal part in this latter specimen a fairly small canal *(aiz)* is seen, which must have transmitted an artery. In *Securiaspis staxrudi* the canal *vizl* is small and runs in postero-ventro-lateral direction (pl. 62:1). In *C. dissimulata* the canal *vizl* (pl. 8:1) divides into two canals postero-ventro-laterally to the opening of the canal d_1. The lateral of these branches runs to the most dorso-posterior region of the inter-zonal part and gives off a branch in dorso-postero-median direction to the lateral side of the dorsal spine (which in this species is rather small).

In *Nectaspis areolata* the canals for both the median and the lateral inter-zonal superficial veins are well developed (pls. 106—107, *vizm, vizl);* the former canal joins the canal d_1. The canals send out numerous transverse branches which partly anastomose and form a network of rather uniform canals in which the main canals often are difficult to discern. Two longitudinal superficial canals *(aiz)* in the median line of the shield between the posterior parts of the canals *vizm* are probably arterial canals (cf. p. 217).

In *Ectinaspis heintzi* the canal *vizm* is represented by three posterior canals which converge to and empty into the canal d_1 (pl. 67:2).

In *Axinaspis whitei* there is formed a complicated network of horizontal superficial canals in the region between the dorsal sensory field and the dorsal crest, and in this network a pair of longitudinal canals *(vizm,* pl. 100:3) can be distinguished, running in posterior direction from the openings of the canals d_1. These canals are seen partly to lie directly beneath the boundaries between two adjacent vascular areas in the exoskeleton (pl. 100:2); the descending vascular canals must have opened into the canals *vizm.*

In *C. exilis* two posterior superficial canals open into the canal d_1 (pl. 11:4). The postero-median one *(vizm)* is the main canal for the median inter-zonal vein, corresponding to the canal *"*nd_1m*"* in a *Cephalaspis* species, described by Stensiö (1927, p. 58; figs. 23—24, 26) while the postero-lateral canal corresponds to his canal *"*nd_1l*"*. In *C. verruculosa* the corresponding postero-lateral canal is more elaborately developed than the postero-median one (pl. 24:2, *vizm).*

For the sake of completeness we shall also mention a groove in the ventral side in the postero-lateral region of the inter-zonal part in *C. doryphorus* (pl. 39:1, 3, *v).* It runs in posterior and slightly median and dorsal direction and consists, more precisely, of two parts, one before and one behind the distal part of the groove *Xll;* the latter part of the groove sends out a median branch, which distally divides into several small grooves. From the way of branching this groove must have lodged a vessel, but as to its nature nothing definite can be said.

We shall now finally in this chapter consider some structures in the dorsal inter-zonal endoskeleton, here interpreted as having lodged nerves.

We have previously accounted for a canal *Xl* which leaves the vagus canal running in straight posterior direction, a canal which is thought to have transmitted a part of the n. lateralis posterior, the main r. lateralis vagi. The canal soon opens into the trunk cavity of the cephalic shield at a variable distance, but not far, behind the postbranchial wall rather near the neural ridge, as seen in *C. oreas, C. excellens,* and *C. doryphorus* (pls. 8:2; 14; 15:1; 17; 39:1, 3) the right canal *Xl* thus pierces the roof of the aortal groove. In some specimens a groove in the ventral face of the inter-zonal endoskeleton continues in posterior direction from the opening of the canal *Xl* (pls. 8:2; 17; 39:1, 3), and in *C. oreas* a second groove runs from this opening in postero-ventro-lateral direction (pl. 8:2). In *C. doryphorus* the longitudinal groove, at least on the left side of the shield, soon divides; a median branch *(Xdl)* is running in posterior direction, while the other, the lateral one *(Xll),* runs in postero-ventro-lateral direction. This latter branch bifurcates near the postero-ventral border of the endoskeleton (pl. 39:1, 3). In the holotype of *C. excellens* no groove is present immediately behind the opening of the canal *Xl* but on the ventral side of the posterior part of the inter-zonal endoskeleton there is a rather short median groove, running backwards, and a somewhat longer lateral groove, running in postero-ventro-lateral direction. These grooves evidently correspond to the median and lateral grooves in *C. doryphorus.* It shall now be noted that in the posterior part of the groove *Xdl* in *C. doryphorus* there is seen on the left side a longitudinal series of minute openings, disposed at slightly varying intervals (the mean distance between two subsequent openings is 0.5 mm). The openings are best seen on the counterpart (pl. 39:3), consisting of a cast of the ventral side of the inter-zonal endoskeleton, as small prominences on the ridge which corresponds to the groove *Xdl.* The openings must have lead into minute dorsal canals running out to the dorsal face of the endoskeleton (and into the exoskeleton).

As the canal *Xl* must have transmitted the main r. lateralis vagi the groove *Xdl* must have lodged a r. dorsalis of this nerve which by fine branches supplied the neuromasts in a dorsal lateral line, and the groove *Xll* a branch supplying the neuromasts in the main lateral line and possibly also an extra-lateral and a lateral line, both on the trunk. It can be noticed that a dorsal lateral line is actually observed in *C. doryphorus* (pl. 40:1, *dlc)* but that no sensory lines have as yet been found on the scale-covered trunk division in any member of the Osteostraci.

The visceral endoskeleton.

The visceral endoskeleton in the Cephalaspids is by Stensiö (1927, pp. 144—145; 1932, p. 37; Holmgren & Stensiö 1936, p. 262) considered to have been composed of two divisions, a dorsal division forming part of the endoskeleton of the cephalic shield, and an independent ventral division consisting of unossified connective tissue.

The dorsal division is said to liee dorsally to the external branchial openings, the ventral one to have been situated ventrally to them. This must, however, mean that the position of the ventral division was morphologically ventral to the external branchial openings as the branchial fossae open on the ventral side of the cephalic shield and the branchial openings lie at the same horizontal level as the plates of the oralo-branchial fenestra. The ventral division of the visceral endoskeleton must thus lie topographically medially to the external branchial openings. Now the ventral parts of the interbranchial septa have approximately this position, and, as we shall see (p. 165), in the living forms they probably continued farther ventro-medially than their preserved parts would indicate. It is most probable that these parts constitute a ventral division of the visceral endoskeleton, corresponding i. a. to those (hypotrematic) parts of the branchial bars in *Petromyzon,* lying ventrally to the external branchial openings (cf. Johnels 1948, pp. 270—271).

The ventral division of the visceral endoskeleton thus formed a direct continuation of the dorsal division but how far it reached in median direction is uncertain. It if reached on to the central parts of the ventral wall of the oralo-branchial fenestra, it probably passed over into some flexible connective tissue, but as to the possible presence of this tissue and its developement we know nothing (cf. Stensiö 1927, p. 144; 1932, p. 41). From what is known of the development of the ventral, hypotrematic, division of the visceral endoskeleton in the Cephalaspids it can only be inferred that it was not independent of the dorsal division but continuous with it and formed part of the cephalic shield.

In the following the visceral endoskeleton will be considered as an entirety without a subdivision into ventral and dorsal portions, and it thus corresponds to the visceral endoskeleton in a "restricted sense" as defined by Stensiö (1927, p. 145). It thus "constitutes a considerable part of the endoskeletal component of the cephalic shield . . . . , forming not only the rostral but also the lateral and to a great extent also the postero-ventral portion of that component. And . . . . , it bounds the oralo-branchial chamber anteriorly, laterally and posteriorly." To this can be added that the roof of the oralo-branchial chamber, as will be evident from the following account, is mostly of visceral origin. As to what parts of this roof in detail (e. g. the aortal groove) belong to the visceral endoskeleton or to the endocranium can not be decided on the basis of the fossils only. All the structures in the roof of the chamber will, however, for the sake of convenience be treated in this connection.

With regard to the different structures in the visceral endoskeleton we shall first consider the canals for the superficial arteries and veins, and the nerve canals and after that, more in detail, the shape of the roof of the oralo-branchial chamber and the different grooves and canals for nerves and vessels which were connected with the branchial apparatus.

The superficial arteries on the dorsal side of the visceral endoskeleton consisted, as far as known, of branches from the a. facialis, a. communicans, a. segmentalis occipitalis, a. marginalis, and possibly also from the a. rostralis.

The intracranial passage of the a. facialis has been considered above. It was said that the main canal *(afac)*, after it had reached the outer part of the endocranium, ran in antero-ventral direction to the dorso-median region of the rostral part of the visceral endoskeleton. It corresponds to the canal for the anterior branch of the a. facialis of Stensiö (1927, pp. 128, 209). The most important branch of the canal *afac* is the lateral one *(aad)* which at first runs in lateral direction just in front of the orbit and then turns backwards along the lateral side of the orbital opening, and which gives off several side-branches *(adl)* to the visceral endoskeleton. In this paper it is called the canal for the a. adorbitalis (p. 62); it corresponds to the main canal for the a. facialis in the terminology of Stensiö.

The side-branches from the canal for the a. adorbitalis to the superficial parts of the visceral endoskeleton extend over an anterior and antero-lateral region of the shield between the orbit and the lateral sensory field, and in some places may reach on to and over this field. They are generally four in number but there is a very great variation as to their development and disposition (cf. Stensiö 1927, figs. 46—47, 49; 1932, figs. 9—12), and I can not find that they are in any way "metamerically" disposed (cf. Stensiö 1927, pp. 132, 182, 214).

The canals will here be called the first to fourth lateral branches of the canal for the a. adorbitalis, and are lettered *adl_1—adl_4*. They correspond more or less exactly, respectively to the "premandibular", the "mandibular", the "lateral infraorbital" and to a lateral side-branch of the "median infraorbital" branch of the canal for the "a. facialis" in the terminology of Stensiö (1927, pp. 129, 132, 209, 211—212). It will, however, be noted that on account of the great variability in their disposition it is often not possible to homologize the canals in different species, and canals with the same lettering in different species are thus not necessarily exactly corresponding.

The first branch *(adl_1*, pls. 10:2; 12:4; 23:2; 29:1; 36—37; 38:2; 62:1; 98:1; 106—107) lies generally between the nerve canal *sel_1* and the vein canal *vcl_1*. In some species it is small and simple, in others ramified, while in still others it seems to be absent. In *Nectaspis areolata* there are several small branches from the canal for the a. adorbitalis, of which a rather large one is lettered *adl_1* (pls. 106—107).

The second branch *(adl_2*, pls. 10:1; 12:4; 19:2; 23; 25:2; 29:1; 36—37; 38:2; 62:1; 98:1; 106—107) leaves the canal *aad* as a rule just medially to the nerve canal *sel_1* and lies either wholly medially to this canal or crosses it and lies with its distal part laterally to it. In some species it issues together with the canal *adl_3* from a common trunk connecting the canals *adl_2* and *adl_3* with the canal *aad*.

The third branch *(adl_3*, pls. 1:2; 6:2; 8:2; 10:1; 12:4-5; 13; 16:1; 23; 36—37; 38:2; 59; 62:1; 63:2; 69:2; 98:1; 106—107) is generally the largest of the side-branches from the canal *aad*. It issues from this canal separately or together with the branch *adl_2*, and usually lies between the nerve canal *sel_1* and the vein canal *vls_3*; it is generally divided into two or three main branches.

The fourth canal *(adl_4*, pls. 6:2; 8:1; 14; 16:2; 23:1; 24:2; 36—37; 38:2; 59) is generally short and lies between the nerve canals *sel_1* and *sel_2*; sometimes it crosses the vein canal *vls_3*. In *C. ibex* (pls. 36:1; 37; 38:2) it is represented by two short branches. It is often missing, and seems in some species to be replaced by the canal for an anterior dorso-lateral superficial artery *(ala_1)*.

We have seen previously (in the chapter on the endocranium, p. 96) that the canal for the a. communicans *(acom)* sends out a canal *(ala)* to the superficial part of the endoskeleton. From its disposition it seems most likely that the canal gave rise to the canals ala_1 and ala_2 for the first and second anterior dorso-lateral superficial arteries. Whether this branch *ala* also gave off some posterior branches for similar arteries or whether they issued from a posterior trunk could not be ascertained in the species examined *(C. signata);* it is, however, evident that all the anterior dorso-lateral superficial arteries issued from the a. communicans. In *C. kozlowskii* (Zych 1937, pl. 2) it is seen that the canals for the four anterior dorso-lateral superficial arteries are branches from a basal trunk, which issues from the canal for the a. communicans. In other species in which the a. communicans passed through the labyrinth cavity the canals for these superficial arteries issue from the vestibulum (cf. Stensiö 1927, figs. 18—19, 23, 25, 27).

The number of the canals for the anterior dorso-lateral superficial arteries is generally four *(*ala_1*—*ala_4*)* but in some species only three such canals are observed and in others there is an additional posterior canal *(*ala_5*)*. The canals are basally connected with each other in different ways as to form basal trunks which join the canal for the a. communicans or the vestibulum. In some species it was impossible to ascertain whether some of the canals belonged to the anterior dorso-lateral superficial arteries (being branches from the a. communicans) or to the posterior dorso-lateral superficial arteries, which issued from the a. segmentalis occipitalis, as they could not be traced to their proximal origin. The canals in question are, however, lettered ala_4 or ala_4*?,* and only those canals which with a fair degree of certainty can be assumed to have carried posterior dorso-lateral superficial arteries are lettered *alp*.

The canals for the anterior dorso-lateral superficial arteries correspond in the main to the canals *"a. sa"* and *"asm"* and its branches in the Cephalaspids described by Stensiö (1927, pp. 181—182, 213—214).

The first canal *(*ala_1, pls. 12:4-5; 16:2; 23; 25:2; 29:1; 36:1; 37; 38:2; 59:1; 60; 106—107) is generally situated behind the vein canal vls_3 and (often) before the nerve canal sel_2; it most often joins the following canal ala_2 to form a common basal trunk. On the left side of the holotype of *C. signata* (pl. 29:1) it lies behind the vein canal vls_4, and in *Nectaspis areolata* (pls. 106—107) it is situated ahead of the canals sel_2 and vls_3. In *C. ibex* (pls. 36:1; 37; 38:2) the basal trunk has an anterior small branch which runs in antero-dorso-median direction to the orbital opening.

The second canal *(*ala_2, pls. 10:2; 12:4-5; 13; 14:1; 16:2; 23:1; 25:2; 29:1; 36:1; 37; 38:2; 59:1; 60; 63:2; 68:3; 106—107) generally lies behind the vein canal vls_4 and before the nerve canal sel_3. As said above, it usually joins the canal ala_1 but in *C. hoeli* (pl. 10:2), *C. sinuata* (pl. 23:1) and an unidentified *Cephalaspis* specimen (pls. 59:1; 60) it fuses with the canal *ala*$_3$, and on the right side of a specimen of *C. excellens* (pl. 13) the canals *ala*$_2$, *ala*$_3$, and *ala*$_4$ unite to form a common basal stem.

The third canal (*ala*$_3$, pls. 6:2; 8:1; 10:2; 23:1; 29:1; 36:1; 37; 38:2; 59:1; 60; 68:3) usually lies between the nerve canals *sel*$_3$ and *sel*$_4$ and before the vein canal *vls*$_5$. It unites with the canal *ala*$_4$ or sometimes, in *C. sinuata* (pl. 23:1), on the right side of a specimen of *C. hoeli* (pl. 10:2), in *Cephalaspis* sp. (pls. 59:1; 60), with the canal *ala*$_2$. In *Nectaspis areolata* is lies immediately ahead of the canal *sel*$_3$.

The fourth canal (*ala*$_4$, pls. 6:2; 8:1; 10:2; 12:5; 13; 16:2; 23:1; 29:1; 37; 38:2; 68:3) is most often situated before the nerve canal *sel*$_4$ but behind the vein canal *vls*$_5$ but lies in some cases behind the canal *sel*$_4$ (pls. 6:2; 12:5). It usually unites basally with the canal *ala*$_3$.

A canal *ala*$_4$? in a *Cephalaspis* sp. (pls. 59:1; 60), lying between the nerve canals *sel*$_4$ and *sel*$_5$ and between the vein canals *vls*$_6$ and *vls*$_7$, and a canal *ala*$_4$?, joining another canal (*ala*$_5$?) in *Securiaspis staxrudi* (pl. 62:1) possibly belong to the system of the posterior dorso-lateral superficial arteries.

In *C. ibex* a fifth canal (*ala*$_5$) issues from the proximal part of the canal *ala*$_4$, runs in posterior direction over the vein canal *vls*$_6$, and divides into a posterior dorsal and a postero-lateral branch (pls. 36:1; 37).

The canals for the posterior dorso-lateral superficial arteries (*alp*) are, as we have seen (pp. 96, 103), branches from the canal for the occipital segmental artery (*as*). This fact could, however, be established with a reasonable degree of certainty, only in *C. kozlowskii* and in *C. signata*.

In *C. excellens* (pl. 16:2) we find a canal (*alp*) leaving the postero-lateral part of the vestibulum and soon dividing into two superficial canals. From what is said above (pp. 99—100), in the chapter on the endocranium, with regard to the groove and the canal *as* and the groove *asb*, compared with the conditions found in *C. kozlowskii* (Zych 1937), it seems most certain that the a. segmentalis occipitalis in *C. excellens* entered the canal *as* (pls. 15:1; 16:1) and, through it, the labyrinth cavity; here it gave off the a. communicans and issued from the vestibulum by the canal *alp*.

The openings into the outer face of the endoskeleton of the superficial branches of the canal *as* are seen on the left side of the shield in the holotype of *C. signata* (pl. 29:1, *alp*).

The canals for the posterior dorso-lateral superficial arteries are two in number (*alp*$_1$, *alp*$_2$); they correspond in the main to the canals "*a. sm*$_2$" and "*a. sp*" in the descriptions by Stensiö (1927; 1932). The first of these canals (*alp*$_1$, pls. 13; 16; 29:1; 36—37) lies, wholly or partly, between the vein canals *vls*$_6$ and *vls*$_7$ and between the nerve canals sel_4 and sel_5. The second canal (*alp_2*, pls. 13; 16; 29:1; 36—37) runs behind the vein canal vls_7. In *C. excellens* and *C. ibex* the canals alp_1 and alp_2 unite on the outer face of the endoskeleton to form a common basal trunk.

A canal *(alp?)* in *Benneviaspis longicornis* (pl. 68:3) possibly lodged a posterior dorso-lateral superficial artery.

The superficial branches *(ams)* from the canal for the a. marginalis (cf. Stensiö 1927, p. 217) are generally short. Some lateral branches are seen in *C. ibex* (pl. 37), and some median branches to the lateral sensory field are exposed in an undeterminable *Cephalaspis* specimen (pl. 60).

Branches of the a. rostralis which went to the most rostral part of the shield or to the rostral process *(Boreaspis robusta,* pl. 78:2) or the a. rostralis itself must have given off small superficial arteries in canals to the outer parts of the shield. Some of the superficial canals on the most rostral part of the visceral endoskeleton are very probably arterial canals issuing from the canal or the groove for the rostral artery or from the transition of this canal or groove to the canal for the a. marginalis, but in this region it is very difficult or impossible to tell the arterial canals from the vein canals if they are not traced to their origin (cf. pls. 8:1; 16:2; 34:1; 38:2, *ars).*

The canals for the superficial veins on the dorsal side of the visceral endoskeleton are well known (cf. Stensiö 1927, pp. 75—76, 118, 132—134, 186—189, 220—225). They belong to the systems of the v. capitis lateralis, the v. marginalis and the v. rostralis (or rostral vein sinus).

The most important of these superficial vein canals are the canals for the dorso-lateral superficial veins (vls_1—vls_8). They will be dealt with here only briefly, and for their disposition on the shield in different species the reader may consult the plates and what is said on each species (in which they are preserved) in the systematic part.

The number of the canals for the dorso-lateral superficial veins seems in general to be six, but not infrequently a seventh canal (vls_7) is observed, in some cases with a posterior branch (vls_8).

The first and second of these canals, vls_1 (pls. 12:4; 16:2; 19:2; 23; 29:1; 34:1; 36:1; 37; 38:2; 62:2; 71:2) and vls_2 (pls. 1:2; 8:1; 11:4; 12:4; 15:4; 16:2; 19; 23:1; 29:1; 34:1; 36:1; 37; 38:2; 67:1; 69:2), join the canal for the preorbital division of the v. capitis lateralis (vcl_1), but in one specimen of *C. excellens* the canal vls_2 opens directly into the orbit (as mentioned above, p. 62; pl. 15:4). In *C. ibex* (pls. 36:2; 37; 38:2) the canal vls_1 is represented by two canals (vls_1a and vls_1b).

In their proximal course some of the third—eighth canals (vls_3—vls_8) most often join in different ways so as to form common basal trunks which open into the canal for the postorbital division of the v. capitis lateralis (*vcl*) or into the postero-dorso-lateral corner of the orbit. Never all the canals are independently developed, and the eighth canal (vls_8) always joins the seventh (vls_7) and can best be regarded as a posterior branch of this canal. The canal vls_3 often joins the canal vls_4 and also in some cases unites with the canal vls_5 to form an anterior common trunk (*vla,* e. g. pls. 8:2; 11:4; 15:4; 71:2), and the canals vls_5 and vls_6 or vls_6 and vls_7 unite to form a posterior common trunk (*vlp,* pls. 10:2; 11:4; 12:5; 13—14; 15:1-2; 16—17; 18:1; 19:2; 23; 61; 68:3; 77:2; 78:3; 95:2; etc.). In *C. signata* there are three basal trunks, the first being formed by the canals vls_3 and vls_4, the second by the canals vls_5 and vls_6 and the third by the canals vls_7 and vls_8. In *C. excellens* and *C. vogti* (certain specimens) all the canals vls_4—vls_7 unite into a common basal trunk (pls. 12:5; 13). The disposition of the proximal parts of the canals is rather varying and often not constant even within the species.

The canal vls_3 is seen in the pls. 1:2; 4:1; 6:2; 8; 10; 11:4; 12:4-5; 13—14; 15:2, 4; 16—17; 19:2; 23; 24:2; 25:1; 29:1; 31:1-2; 32:1, 3; 36—37; 38:2; 59:1; 60; 62:1; 63:2; 64:2; 67:1; 68:3; 69:2; 70; 71:2; 77:2; 78:3; 90:3; 91:1; 93:2; 98:1; 106—109. In the genus *Cephalaspis* the canal generally opens into the postero-dorso-lateral corner of the orbit; in *C. signata,* however, it joins the canal vls_4, and the common trunk thus formed, opens into the canal for the postorbital division of the v. capitis lateralis (*vcl*) just behind the orbit (pl. 32:2). Similar conditions have also, as an exception, been observed in *C. excellens.* In *Securiaspis staxrudi* the canals vls_3, vls_4 and vls_5 unite to form a short and wide basal trunk which opens into the canal *vcl* most anteriorly but also with the foremost part into the postero-dorsal corner of the orbit (pl. 62:1); in *S. quadrata* the canal vls_3 opens in about the same way as this common trunk (pl. 64:2); in an undeterminable *Securiaspis* specimen the canal vls_3 opens into the orbit (pl. 63:2). In *Ectinaspis* the canal vls_3 runs to the postero-dorso-lateral corner of the orbit (pl. 67:1). In *Benneviaspis* the canal vls_3 (or the common trunk formed by the union of this canal and the canal vls_4) opens into the orbit (pls. 68:3, left side; 70:2; cf. pl. 71:2) or into the canal *vcl* behind the orbit (pl. 70:1). In *Tegaspis, Boreaspis* (pls. 78:3; 90:3; 91:1; 93:2), *Axinaspis* (pl. 98:1), *Acrotomaspis, Nectaspis* (cf. pls. 106—109), and also in *Hoelaspis* (pl. 77:2; cf. Stensiö 1927, pl. 45) the canal vls_3 joins the canal *vcl* behind the orbit.

The canal vls_4 is observed in many specimens (pls. 1:2; 4:2; 6:2; 8:1; 10:2; 11:4; 12:5; 13; 15:4; 16; 19:2; 23; 24:2; 25:1; 29:1; 32:1-3; 36—37; 38:2; 59:1; 60; 62:1; 64:2; 67:1; 68:3; 69:2; 70:2; 71:2; 77:2; 78:3; 106—109) as well as the canal vls_5 (pls. 4:2; 13; 16; 19:2; 23; 25:1; 29:1; 32:1; 36—37; 38:2; 59:1; 60; 62:1; 67:1;

68:3; 69; 70:2; 71:2; 77:2; 78:3; 106—109) and vls_6 (pls. 4:2; 6:2; 8:1; 10:2; 12:4-5; 13—14; 16; 19:2; 23; 25:1; 29:1; 32:1; 36—37; 59:1; 60; 62:1; 64:2; 67:1; 68:3; 69:2; 70:2; 71:2; 77:2; 78:3; 100:1; 106—107). The canal vls_7 is seen in the pls. 10:2; 12:5; 13; 16; 23; 29:1; 36—37; 59:1; 60; 69:2; 77:2; 100:1.

In *C. signata* the canal vls_7 has a rather considerable posterior branch (vls_8, pl. 29:1); in *C. ibex* the corresponding canal is small (pls. 36:1; 37, vls_8).

In their distal course the canals for the dorso-lateral superficial veins have a fairly constant disposition in relation to the canals for the nerves of the lateral sensory fields. The canals vls_1 and vls_2 lie medially to the canal sel_1, the canal vls_2, however, in *Cephalaspis* often between the branches sel_1a and sel_1p; the canal vls_3 lies just in front of the canal sel_2, the canal vls_4 between the canals sel_2 and sel_3, the canal vls_5 between the canals sel_3 and sel_4 and the canal vls_6 between the canals sel_4 and sel_5; the canals vls_7 and vls_8 lie generally behind the proximal part of the canal sel_5. Although the canals thus alternate rather regularly with the nerve canals to the lateral sensory fields, they have no such relation to the canals for the branchial nerves, and they cannot in any way be said to have a "metameric disposition" (cf. Stensiö 1927, p. 225).

In an undeterminable *Cephalaspis* specimen (pls. 59:1; 60) we find some aberrant conditions with regard to the canals for the dorso-lateral superficial veins. The canal vls_5 has in its inner half an anterior branch (vls_4m) which represents the basal part of the canal vls_4. Between the distal parts of the nerve canals sel_2 and sel_3 runs a vein canal (vls_4l) which in proximal direction turns backwards and opens into the canal vls_5; it is probably the distal part of the canal vls_4 which has lost its connection with its basal part and acquired a new, more distal one with the canal vls_5. The canal vls_6, basally joined to the canal vls_5, is by a large sinus-like canal *(vcom)* in communication with the canal *vco* in the shoulder-girdle. By these connections a longitudinal superficial vein canal passage is formed, lying medially to the posterior part of the lateral sensory field.

In the anterior part of its course the v. capitis lateralis (or the preorbital division of this vein) was a superficial vein which drained the antero-dorso-median part of the ethmoidal region and the rostral visceral part, lying immediately in front of this region (cf. Stensiö 1927, pp. 118, 132, 225, 228); its canal vcl_1 is seen in many specimens (pls. 3:2; 6:2; 8:1; 10; 15:2; 16:2; 19:2; 23; 29:1; 36:1; 37; 38:2; 62:1; 63:2; 67:1; 71:2; 77:2).

Median branches *(vms)* from the canal for the v. marginalis *(vmarg)* run to the lateral sensory field and to the region of the shield lying just medially to this field (pl. 60).

The dorsal superficial branches *(vrd)* from the canal or groove for the rostral vein or vein sinus to the rostral part of the visceral endoskeleton between the anterior part of the lateral sensory fields are seen in several specimens (pls. 6:2; 8:1; 9:6; 13—14; 16:2; 18:2; 20:2; 29:1; 34:1; 36:1; 37; 38:2; 61; 64:1; 70:1). In *Nectaspis areolata* this part of the shield is provided with a superficial network of anastomosing canals in which the individual canal trunks cannot be distinguished, nor can it be made out which of the canals are vein canals and which are arterial canals (pl. 110:1).

Turning now to the nerve canals we shall here consider their course through the visceral endoskeleton with the exception of those parts of the nerves which went into the oralo-branchial chamber and left impressions in the roof of this chamber and which will be considered later on in this chapter.

We have previously (p. 60) found that the n. profundus evidently was a very small nerve which probably supplied only the interorbital space and the superficial part of the ethmoidal region and possibly also a part of the rostral visceral endoskeleton. There is no canal which without any doubt can be exclusively assigned to this nerve but some canals (lettered V_1*?,* pls. 10:1; 37; 38:2) in *C. hoeli* and *C. ibex* are possibly canals for branches of this nerve; a canal V_1*?* in *Nectaspis areolata* is with much doubt thought to be a canal for such a branch.

The r. maxillaris trigemini left the orbit through a canal of its own *(*V_2*);* this canal or parts of it is seen in many specimens (pls. 3:2; 4:1; 6:2; 8:2; 9:7; 10:2; 11:4; 14; 15:3-4; 19:2; 23:2; 25:2; 30:1; 36—37; 38:2; 61; 62:1; 63:2; 64:2; 66; 67:1; 68:3; 69:2; 70; 71:2; 77:2; 78:1; 81:1; 82:2; 83:1; 84:2; 86:2; 89:2; 90:3, 5; 93—95; 97:3; 98:1; 100:1; 102:1; 103:4; 106—107; 110). After its origin from the antero-ventral part of the orbit it ascends to the outer part of the rostral visceral endoskeleton and here runs in antero-ventral direction until it enters the oralo-branchial chamber with one or several openings; this takes place about midway between the orbit and the rostral margin of the shield *(C. excellens,* pl. 13) or nearer to this margin *(C. exilis,* pls. 11:4; 27:1; *C. retusa,* pl. 9:5; *C. signata,* pls. 29:2; 30:1; *Boreaspis* spp., pls. 83; 85; 87:1; *Nectaspis areolata,* pls. 108—109). In *Securiaspis staxrudi, Boreaspis costata* and *B. macrorhynchus* the canal V_2 during its superficial course divides into two branches *(*V_2l*,* V_2m*,* pls. 61; 62:1; 94:2; V_2, pls. 86:2; 93:1), and at least in the latter species the median branch (which bifurcates) runs to the superficial parts of the shield. The canal sends out narrow branches to the superficial part of the visceral endoskeleton (pls. 93:1; 94:2; 97:3) and some of its terminal branches end near the rostral or antero-lateral margin of the shield (pls. 30:1; 94:1). These branches must have carried somatic sensory fibres or, more specifically, general cutaneous fibres. Such fibres were, however, without doubt, also present in the nerve branches which went through the roof of the oralo-branchial chamber on to the roof of the mouth cavity (cf. the conditions in *Petromyzon,* Johnston 1905a, p. 184; Lindström 1949, pp. 372—373); for the rest the nerve branches to the oralo-branchial chamber carried visceral motor fibres for the oral musculature. In some specimens the visceral endoskeleton is so thin that the canal V_2 produced a ridge (pV_2) in the roof of the oralo-branchial chamber (pls. 9:6; 15:4; 27:1; 96:1; 108—110).

The r. mandibularis trigemini (V_3) which, as we have seen (p. 65) was a pure motor trunk, generally passed through the orbit before it entered a canal running out to the visceral endoskeleton, but in *Nectaspis* it went in a canal of its own directly from the antero-median part of the labyrinth cavity. The canal V_3 sometimes also gave passage to lateralis fibres coming from the anterior lateralis ganglion in the trigeminus-lateralis chamber. In general the canal V_3 runs for a short or rather long distance through the outer parts of the visceral endoskeleton before it opens into the oralo-branchial chamber (the canal is more or less distinctly seen in several specimens: pls. 3:2; 8:2; 10:2; 61; 62:1; 63:2; 68:3; 69:2; 70; 71:2; 78:3; 86:2; 89:2; 91:2; 93:2; 94—95; 97:1, 3; 100:1; 102:1; 103:4; 106—109; its opening into the oralo-branchial chamber is exposed in the specimens figured in pls. 9:6-7; 13—14; 16:1; 27; 29; 78:2-3; 81:2; 82:1; 83; 85; 87:1; 91; 93:1; 94:2; 95—96; 108—109; 110:1). In *Cephalaspis* the canal V_3 is short or very short and does not (or only exceptionally) enter the dorsal face of the endoskeleton, but in other genera in which it is observed *(Securiaspis, Tegaspis, Ectinaspis, Benneviaspis, Hoelaspis, Boreaspis, Kiaeraspis, Acrotomaspis, Nectaspis)* it has a rather long passage through the visceral endoskeleton. In *Cephalaspis* the canal generally opens into the oralo-branchial chamber in the interval between the two branches of the canal sel_1 or *(C. excellens, C. vogti* in which this canal is undivided) just in front of the canal sel_1. In *Securiaspis* it passes down between the branches of the canal sel_1 or entirely behind or ventrally to this canal. These two conditions are also present in *Tegaspis, Benneviaspis, Hoelaspis, Boreaspis, Axinaspis, Acrotomaspis* and *Nectaspis* (see also p. 239).

The canal for the n. facialis *(VII)* issues from the lateral part of the vestibulum. The main canal *VII* in *Cephalaspis* is very short and does not reach the outer part of the endoskeleton; it opens into the oralo-branchial chamber rather far dorso-medially just anteriorly to the canal sel_2; because of its deep position in the endoskeleton it is seldom exposed (pls. 10:2; 14; 15:1; 27:2; 29:2). In *Securiaspis* (pl. 61), *Benneviaspis* (pl. 71:2), *Hoelaspis* (pl. 77:2) and *Axinaspis* (pl. 100:1) it is somewhat longer and in *Boreaspis* (pls. 81:2; 82:1;

83:2; 85; 86:2; 87:1; 91:1; 93; 94:2; 95—96), *Acrotomaspis* (pl. 103:1) and *Nectaspis* (pls. 106—109) it is very long, opening far antero-ventrally into the oralo-branchial chamber. It normally lies closely anteriorly to the canal sel_2 but in *Acrotomaspis* (pl. 103:1) runs closely behind this canal. The n. facialis was, as the following cranial nerves, mainly a nerve for the branchial pouch. The general cutaneous component of the nerve was apparently feebly developed (see below) and there was very probably no (normally developed) lateralis component accompanying it.

The canals for the n. glossopharyngeus *(IX)* have been accounted for above (in the chapter on the endocranium). Here it will only be repeated that the canal for the main nerve (the branchial ramus) in *Cephalaspis* either runs posteriorly and laterally to the labyrinth cavity or consists of two independent canals, a proximal one behind, and a distal one laterally to the labyrinth cavity; the distal canal is very short (in this latter case the nerve passed through the vestibulum). The canal runs closely associated with or is coalescent with the canal for the a. communicans (pls. 4:1; 14; 15:1; 16:1; 31:1-2, 6; 32:1-2) and opens far dorso-medially into the oralo-branchial chamber (pls. 16:1; 27; 29:2; 32:1). In the other genera the canal *IX* or, more exactly, its opening rather far ventro-laterally into the oralo-branchial chamber, has been observed in *Boreaspis* (pls. 81:2; 83:2; 87:1; 93; 96:2), and a canal which possibly is the canal *IX* is exposed in *Acrotomaspis* (pl. 102:1, *IX?)* and *Nectaspis* (pl. 107, *IX?).* In this latter genus the n. glossopharyngeus ran in a canal behind the labyrinth cavity, much in the same way as in *C. signata* (fig. 12; pl. 112:1). In *Boreaspis* the canal runs ventrally to the canal sel_3 and its opening into the oralo-branchial chamber lies just anteriorly to this canal. In *Cephalaspis* it opens downwards in the interval between the proximal parts of the canals sel_2 and sel_3. The canals for somatic sensory nerve fibres of the glossopharyngeal nerve are known only in *C. signata* (see above, p. 93), and superficial canals possibly having carried such fibres will now be considered in connection with other superficial nerve canals.

Before doing so we shall only recall that the canals for the n. vagus have been dealt with in connection with the occipital region of the endocranium and will be further considered below when dealing with the branchial fossae in the oralo-branchial chamber. No canals in the visceral endoskeleton for somatic sensory branches of the n. vagus are known (cf. Stensiö 1927, pp. 165, 191).

When dealing with the ethmoidal and orbito-temporal regions of the endocranium some narrow grooves in the floor of the orbit and some canals issuing in antero-lateral direction from the orbit have been mentioned, and following Stensiö (1927), these canals have been considered to have carried somatic sensory fibres. Some of them were general cutaneous and others lateralis fibres. Now we find in *C. excellens* that some of these canals continue in antero-ventro-lateral direction in the outer parts of the visceral endoskeleton, in some cases on to the median margin of the lateral sensory field (pls. 14, n_1; 16:2, *n).* In *C. vogti* a similar canal *(bu,* pl. 12:5) runs first along the lateral border of the orbital opening and then turns in antero-ventro-lateral direction; it has exactly the same course as the proximal part of the infraorbital groove of the sensory line system, and it had, beyond any doubt, carried a lateralis branch which supplied this line. In *C. exilis* (pl. 34:1) we find the distal continuation of this nerve canal: a narrow canal *(bu)* issues from the canal sel_1 near the median margin of the lateral sensory field and runs in anterior direction over the foremost part of this field bifurcating into an antero-median and an antero-lateral canal. The former branch is assumed to have given passage to a nerve branch supplying the antero-median part of the infraorbital line, while the latter branch possibly carried a lateralis branch for a supposed anterior marginal line (this line has not yet been observed in any Cephalaspid but is present in some other Osteostraci). A canal corresponding to the antero-median branch of the canal *bu* in *C. exilis* is seen in *C. divaricata* (pl. 6:1, *bu),* its median part following the main course of the groove ifc_1 of the sensory line system. In *C. ibex* (pls. 36:1; 37) and in an undeterminable *Cephalaspis* specimen (pls. 59:1; 60) there are several narrow superficial canals *(n)* which, on account of their course and mode of branching must have given passage to nerve branches, and, more specifically, to somatic sensory nerves. The anterior ones of these canals in *C. ibex,* that is, those lying behind the canals V_2 or vls_1b but ahead of the canal vls_4, have such a position that they must have carried nerve branches originating from the trigeminus-lateralis-ganglion complex; the nerves in the canals *n* between the canals vls_4 and vls_6 were branches of the n. facialis or the n. glossopharyngeus, while the nerves in the posterior canals *n* most probably were cutaneous branches of the n. glossopharyngeus.[1] It seems thus as if the general cutaneous component in the n. facialis, if present at all, was rather feebly developed. Which of the canals in question had carried general cutaneous fibres and which of them carried lateralis fibres can not yet be decided.

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[1] Cf. the course of the canals *IXla* and *IXlp* and the superficial canals very probably issuing from the canal IX_1 in *C. signata,* see pp. 91, 93; it will here be noted that the canals *IXla* and *IXlp* reached the outer face of the endoskeleton ventro-laterally to the posterior half of the dorsal sensory field or just dorso-medially to the union of the canals vls_7 and vls_8, and that the canals *n* from the canal $IX + acom$ reach the dorsal face of the endoskeleton somewhat postero-laterally to the orbit.

We have yet another kind of superficial nerve canals to account for, viz. the canals for the lateral sensory fields. They are generally most conspicuous and more or less perfectly preserved in all specimens in which the visceral endoskeleton is not destroyed. The canals for these nerves are generally broad and flattened but sometimes (as e. g. in *C. eurhynchus,* pl. 4:1, and especially in *C. kozlowskii,* Zych 1937, pl. 2) they are more rounded in cross-section and somewhat similar to other nerve canals. They are, however, always larger than other canals and the nerves in them must have been very strongly developed, hypertrophied.

We have previously found that in some species the canal sel_1 has a fairly independent position in relation to the other nerve canals *sel,* and that it was provided with a distinct basal swelling, doubtless caused by a ganglionic mass. This fact and the conditions in several species and genera as e. g. *Boreaspis, Kiaeraspis, Nectaspis* and in other Osteostraci make it much more probable that this canal enclosed a single nerve branch which in some cases bifurcated distally than two nerves (as supposed by Stensiö 1927, pp. 84; 171—172), and this is assumed here (the canal is lettered sel_1, and its distal branches sel_1a and sel_1p, and these branches thus correspond to the canals "sel_1" and "sel_2" of Stensiö).

The total number of nerve canals for the lateral sensory field (or fields) was thus five in both the Cephalaspids and most of the older Osteostraci. Exceptions may, however, occur. Thus in a specimen of *Boreaspis macrorhynchus* we find an additional nerve canal (sel_2b) and consequently in this specimen six nerve canals for the lateral sensory field (pl. 95:2).

In all the specimens of the Spitsbergen Cephalaspids, so far examined, the proximal course of the canal sel_1 is constant and very characteristic. Issuing from the anterior or antero-lateral part of the vestibulum it runs mainly in antero-lateral direction to the lateral margin of the orbit and follows this margin to the antero-lateral corner of the orbit; here it turns in antero-ventro-lateral direction and enters the visceral endoskeleton. In most of the *Cephalaspis* species it bifurcates near the antero-lateral corner of the orbit and there are thus two branches of the canal which enter the visceral endoskeleton. In *C. excellens* (pls. 13; 15:2; 16:1), *C. vogti* (pl. 12:5), and a specimen of *C. dissimulata* (pl. 8:1) the canal runs undivided on to or near to the lateral sensory field. In *Securiaspis* (pls. 61; 62:1; 63:2; 64) and *Tegaspis* (pl. 66) the canal sel_1 divides into two branches about midway between the orbit and the lateral sensory field, or somewhat nearer to this field. In *Benneviaspis* (pls. 69:2; 71:2), *Hoelaspis* (pl. 77:2) and *Ectinaspis* (pl. 67:2) the canal branches in general just medially to the lateral field, and in *Boreaspis* (pls. 82:2, 4; 83; 86; 89:1-4; 90:3-5; 91; 93—95;

96:2), *Kiaeraspis* (pl. 97:1-3), *Axinaspis* (pls. 98:1; 100:1), *Acrotomaspis* (pls. 101:1; 102:1-2; 103:1-2, 4; 105:4) and *Nectaspis* (pls. 108—109; 111:3-4) it is virtually undivided. In a specimen of *Boreaspis robusta* the canal sel_1, as an exception, bifurcates midway between the orbit and the lateral field (pl. 78:3).

When, as in *Kiaeraspis* (pl. 97:2), *Boreaspis* (fig. 93) and *Axinaspis* (fig. 101B), the lateral sensory fields are subdivided into two parts the anterior field is supplied with two nerve canals and the posterior one with three canals. In *Nectaspis* (fig. 105C) the anterior and the middle field receive two canals each and the posterior field one canal. In *Acrotomaspis* (fig. 102B) the first, second and third fields each receive one nerve canal and the fourth field two nerve canals.

We shall now turn to a consideration of the roof of the oralo-branchial chamber in different Cephalaspids and the various impressions produced in it mainly by the branchial apparatus and by diverse structures related to this apparatus.

We shall then first consider in some detail the conditions in the roof of the oralo-branchial chamber in the genus *Cephalaspis,* and shall turn our attention to a fairly well preserved cast of the oralo-branchial chamber in the holotype of *C. signata* (pls. 29:2, detail in pl. 27:2; the most anterior part of the roof of this chamber is also shown from below in pl. 30:1; cf. also fig. 14).

The aortal ridge, present only in the anterior part of the roof, is very high and keel-like with blunt edge, and without any aortal groove (cf. *C. salweyi,* Stensiö 1932, p. 38; pl. 25:1). Anteriorly but at some distance behind the rostral part of the ventral rim it becomes low and broad-backed, and disappears gradually. Somewhat behind its anterior end a pair of low, broad and indistinct ridges runs from it in antero-ventro-lateral direction for a short distance but is soon wholly obliterated, at least on the right side; on the left side the first branchial fossa behind it is somewhat better pronounced and deeper in front than the right one, and its anterior border forms a rather slightly developed margin which runs antero-laterally as a continuation of the ridge referred to. The rostral area ahead of the aortal ridge is quite plane and not in the least depressed. There is thus formed a large but indistinctly bounded triangular anterior area, the face of which is fairly smooth, and (this must be emphasized) which has no cavity or fossa in its ventro-lateral corners, where it passes imperceptibly over into the ventral rim.

The pair of short ridges, just mentioned, corresponds to the well developed velar ridge in *Nectaspis,* to be described later on (p. 155); and this term will be employed for them also in *Cephalaspis.* The anterior triangular area corresponds to the area occupied by the buccal cavity in *Nectaspis.* This area in *Cephalaspis* will here be termed the buccal area (area buccalis); its supposed exoskeletal bone covering is called by Stensiö (1932, p. 37) the maxillary toothplate. It will, however, be observed that no such exoskeletal covering is present in any of the examined Cephalaspids from Spitsbergen.

In the anterior part of the oralo-branchial chamber behind this area (in the branchial chamber proper) the interbranchial ridges are rather poorly developed, being fairly distinct only near to the aortal ridge and in their ventro-lateral parts in passing over into the interbranchial septa. The branchial fossae are defined and separated from each other, as will be seen, mainly by the development of other structures.

The first branchial fossa is very large, roughly triangular in outline with the apex dorso-postero-medially near the median line at a transverse level with the anterior end of the circum-nasal fossa. On the right side it passes without boundary antero-ventro-laterally over into the buccal area; for the rest it is limited anteriorly by the pair of velar ridges, mentioned above, and posteriorly its borders are represented by the first interbranchial ridge, the posterior margin of the groove aq_1 (see below) and the first interbranchial septum. The left branchial fossa 1 is somewhat shorter than the right one.

The most conspicuous feature in the first branchial fossa is a transverse series in the posterior part of the fossa of eight oblong closely lying impressions or pits *(igl)* separated from each other by narrow ridges *(gl)*. The series of pits begins in the dorso-median part of the fossa rather near to the aortal ridge and reaches in antero-ventro-lateral direction to a point some distance from the ventral rim. Each of the pits extends antero-medially to postero-laterally. The most median (the first) pit is the smallest one, and is rather indistinctly defined, the second and the third are somewhat larger then the first but still slightly smaller than the five subsequent ones which are of about uniform size. The first five pits are all fairly well bordered on all sides but the three last ones pass postero-laterally over into a transverse broad groove (aq_1). The series of pits is separated from the posterior border of the fossa by an area of about uniform breadth. This area is rather plane in its dorso-median part but is ventro-laterally somewhat deepened so that the fairly broad and shallow groove (aq_1), just referred to, is formed between the transverse series of pits and the posterior border of the first branchial fossa. The groove continues antero-ventro-laterally but most distally there is formed from the branchial fossa a postero-lateral continuation in the shape of an external groove *(dext)* running along the inner border of the ventral rim. This external groove lies laterally (or ventro-laterally) to the interbranchial septum bordering the fossa postero-ventro-laterally (cf. Stensiö 1927, fig. 33). It is to be noted that the external groove is not uniform (and this applies also to the external grooves from the two following branchial fossae) but that its postero-lateral part is somewhat more depressed and forms a fairly distinct impression *(dexta).* The roof of this impression is traversed by a longitudinal branching groove *(a)* which passes over posteriorly into a small canal running to the canal for the a. marginalis. The antero-median part of the external groove from the first branchial fossa disappears at about the first third of the length of the ventro-lateral part of the second fossa; the postero-lateral impression *(dexta)* continues to somewhat more than the middle of this distance. The anterior part of the corresponding impression *(dexta)* in the second external groove has a branching transverse groove.

In the most ventro-lateral part of the branchial fossa, distally to the transverse series of pits *(igl),* there is a fairly large, oblong impression (th_1) with uneven borders. On the left side of the shield this impression is very shallow; on the right side it is somewhat larger than on the left side, and slightly deeper and indistinctly bi-lobed. The bottom of the impression is not smooth but in places very finely granulate and for the rest provided with minute branching grooves and ridges.

Along the anterior border of the transverse row of pits *(igl),* and thus in the middle of the first branchial fossa, runs a rather long groove *(pbg);* it begins medially just ahead of the first pit or, on the left side, somewhat medially to this pit, and is here fairly narrow but becomes gradually somewhat deeper and broader in antero-ventro-lateral direction. It can be traced to a point before the last pit. In its distal part it is, however, indistinct and without any clear border on its anterior side. In the median half of its length the groove shows some very faint cross-ridges, one just in front of each ridge *gl.* The groove *pbg* does not ramify or send out any secondary branches during its course.

The second branchial fossa is of fairly uniform breadth. It is bordered anteriorly by the first interbranchial ridge and by the posterior margin of the groove aq_1, and, most ventro-laterally, by the first interbranchial septum; its posterior border is formed by the second interbranchial ridge, the posterior border of the groove aq_2, and the second interbranchial septum. The second interbranchial ridge passes medially over the orbital prominence (pl. 32:2-3, ibr_2, *prorb).*

In the dorso-median part of the fossa the pits *igl* are generally very indistinctly defined. In the ventro-lateral part of the fossa they are developed as fairly narrow grooves, separated by rather flat ridges which are somewhat broader than the grooves; the grooves pass over into the transverse groove aq_2 and can be regarded as secondary branches from this groove.

The groove aq_2 is better developed than the corresponding groove aq_1 in the first branchial fossa. It begins in the dorso-median third

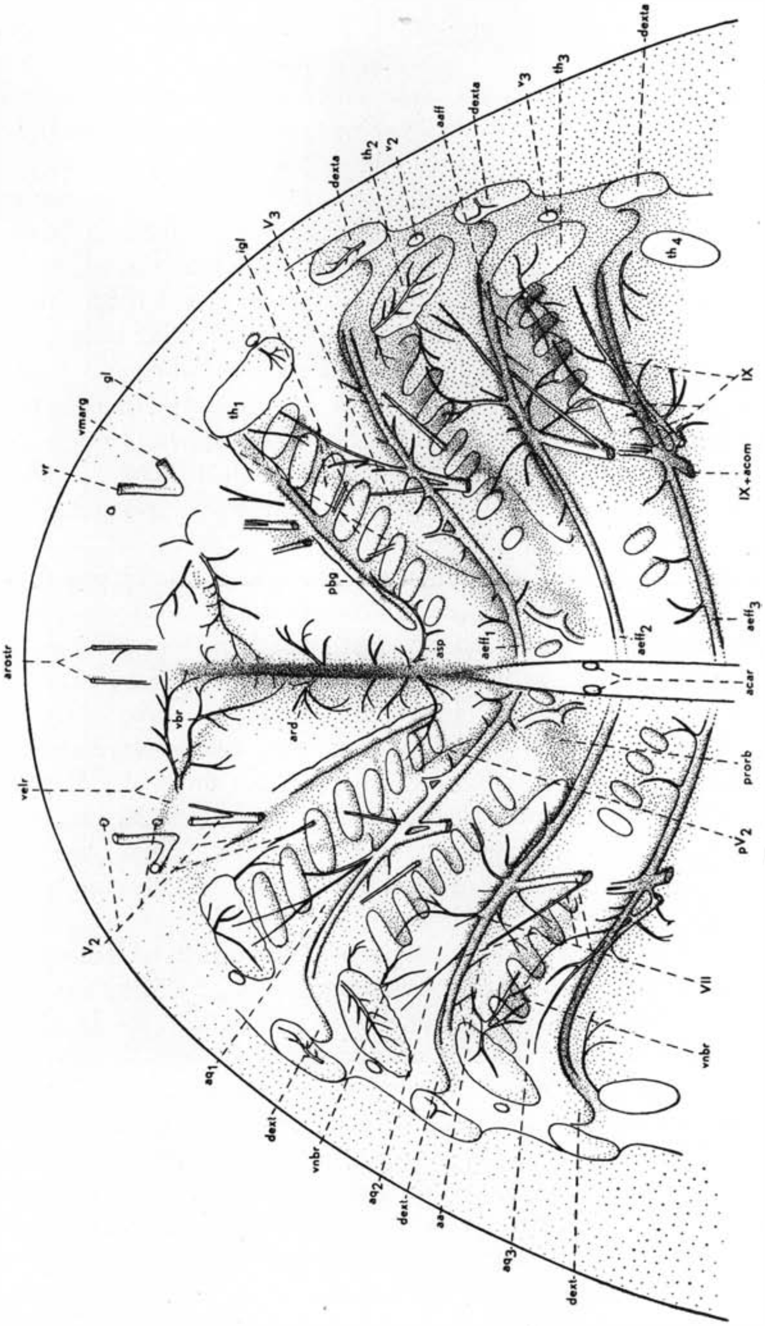

Fig. 14. — *Cephalaspis signata.* Cast of the anterior part of the oralo-branchial chamber; dorsal view. (Diagrammatic figure showing the impressions in the roof of the chamber.) × 1½.

aa, grooves for afferent arterioles; *aaff,* groove for an afferent branchial artery; *acar,* canals for the a. carotis; $aeff_1$—$aeff_3$, grooves for the first to third efferent branchial arteries; aq_1—aq_3, grooves probably for efferent ducts in the first to third gill-sacs; *ard,* grooves for dorsal branches of the a. rostralis (impar); *arostr,* canal and grooves for the a. rostralis (par); *asp,* grooves for the a. spiracularis; *dext,* groove for the external efferent duct from the gill-sac; *dexta,* impression for a structure of unknown significance near the external branchial duct; *gl,* ridges in the branchial fossa, probably for the attachment of the gill-lamellae; *igl,* grooves or pits in the roof of the branchial fossa between the ridges *gl; pbg,* groove probably for the peripharyngeal ciliated groove; *prorb,* impression of the otical prominence; pV_2, impression caused by the ridge enclosing the r. maxillaris V; th_1—th_4, impressions probably for the gl. thymus; *vbp,* grooves for the v. bucco-pharyngealis; *velr,* impression of the velar ridge; *vmarg,* canal and groove for the v. marginalis; *vnbr,* grooves for vv. nutritiae branchiales; *vr,* canal and groove for the v. rostralis; v_2—v_3, canals for the second and third ventral transversal veins; V_2, grooves and canals for branches of the r. maxillaris V; V_3, grooves for branches of the r. mandibularis V; *VII,* grooves for branches of the n. facialis; *IX,* grooves for branches of the n. glossopharyngeus; $IX + acom$, groove for the main branch of the n. glossopharyngeus and for the a. communicans.

of the fossa, where it is bordered anteriorly by a ridge caused by the r. mandibularis V (pl. 27:2, pV_3). Ventro-laterally it becomes gradually broader and deeper and passes distally over into a shallower, postero-laterally directed external groove.

No groove corresponding to the groove *pbg* in the first branchial fossa is present in the second fossa.

A distinct and fairly deep impression (th_2), equivalent to the impression th_1 in the first fossa, in the ventro-lateral part of the second fossa and somewhat dorso-medially to its ventral end occupies almost the entire breadth of the fossa. The bottom of the impression is uneven and in the median line traversed by a groove with numerous side-branches.

The third branchial fossa is slightly shorter than the second fossa. It is bounded anteriorly by the second interbranchial ridge, the posterior border of the groove aq_2 and the second interbranchial septum, and posteriorly by the well developed third interbranchial ridge (which also partly forms the posterior margin of the groove aq_3) and the rather high third interbranchial septum. The third interbranchial ridge reaches medially over the most anterior part of the otical prominence. The fossa can be regarded as consisting of two parts, a short dorso-median, horizontal part, lying beneath the endocranium and a long distal part in the ventro-lateral sloping division of the roof of the oralo-branchial chamber.

On the horizontal part of the fossa four oblong pits are observed on the left side, the two median ones are rather small; on the sloping part of the right side four indistinct pits can be discerned. They are developed like those in the second branchial fossa and thus as grooves, opening into the transverse groove aq_3, separated from each other by fairly broad intervening spaces.

The groove aq_3 along the posterior margin of the fossa is well developed and almost as long as the groove aq_2 but is in its ventro-lateral part slightly narrower and considerably deeper than the latter. Like the two grooves in the first and second fossae the groove aq_3 passes over into a shallow postero-laterally directed external groove which here is somewhat narrower and shorter than the preceding ones.

The impression th_3 in the ventro-lateral part of the branchial fossa is well defined and rather deep but somewhat smaller than the impression th_2. Its bottom is provided with short irregular grooves and ridges of which one is somewhat larger than the others and runs, soon bifurcating, for a short distance from its dorso-median margin in ventro-lateral direction.

The fourth and following branchial fossae are very imperfectly or not at all preserved in the specimen examined. They are, however, in good condition in a specimen of *C. exilis,* to be described below (p. 148). In this connection shall only be mentioned that the fourth interbranchial ridge, which borders posteriorly the fourth fossa, medially ends on the middle part of the otical prominence.

After having described the general features of the roof of the oralo-branchial chamber, we shall now, before giving an account of the many grooves for nerves and vessels found in this roof, put forward an attempt at an interpretation of the different structures met with so far.

That the different compartments in the oralo-branchial chamber, here (after Stensiö 1927) called branchial fossae, really had lodged the respiratory apparatus seems beyond any doubt (Stensiö 1927, pp. 46, 166—170), and it is also evident that the gills of the Cephalaspids, as pointed out by Stensiö (1927, pp. 46, 167, 169—170) must have been somewhat similar to those of recent Cyclostomes, particularly those in the Petromyzonts. And if this be true, the series of pit-like impressions *(igl)* in the roof of the oralo-branchial chamber as well as the grooves *aq* and *dext* must have been caused by the gill apparatus. The interbranchial ridges in the Cephalaspids correspond to the dorsal (epitrematic) part of the branchial arches in the Petromyzonts (Stensiö 1927, pp. 165—166) and they thus each formed the basis of the gill-septum from which an anterior hemibranch was developed into the branchial fossa in front of the interbranchial ridge, and a posterior hemibranch into the next fossa behind the same interbranchial ridge. A complete gill-pouch in a branchial fossa was thus composed of gills developed from the sides of two subsequent gill-septa (interpreted after the conditions in *Petromyzon).* In *Petromyzon* there arise from the gill-septum an anterior and a posterior series of processes, the gill-lamellae, and from each of these lamellae grow out a dorsal and a ventral row of secondary gill-lamellae. The dorsal and ventral gill-lamellae in the gill-pouch are united with the wall of the gill-pouch and have coalesced with the corresponding gill-lamellae from the adjacent gill-septum in the same gill-sac (Dohrn 1885, fig. 17; Nestler 1890, pp. 6—8; figs. 1—2, 5—6; Schaffer 1895b, pp. 295—296; Gaskell 1898, figs. 1—2; pl. 3; 1908, figs. 63—64, 68; Goette 1901, pp. 535—546; figs. 24—30; Vialleton 1908, pp. 59—67; Jacobshagen 1920, pp. 111—116; Keibel 1927, figs. 12—13; Sakwarelidse 1928; Daniel 1931, p. 46; fig. 2; Balabaj 1935a; Rauther 1937b, pp. 218—221). By comparison between the structure of the branchial fossae of the Cephalaspids and the structure of the gills in *Petromyzon* it seems most plausible that in the transverse series of groove- or pit-like impressions in the roof of each branchial fossa the ridge *(gl)* between two adjacent pits *(igl)* had formed the basis of a gill-lamella which was developed in the soft tissue in the ventral continuation of this ridge. The gill-sacs (or more correctly the dorsal halves of the gill-sacs) had extended very far dorso-medially or to near the aortal ridge (cf. *Petromyzon,* e. g. Vialleton 1903, p. 305; Goodrich 1909, fig. 35). The space ventro-laterally between the interbranchial septa was occupied only by the external efferent ducts.

It is most interesting to find that in some Poraspids (in the group Heterostraci) the transverse branchial impressions are in a way, similar to that just described in *C. signata,* subdivided by a series of oblong longitudinal pits *(Poraspis polaris,* Kiær & Heintz 1935, p. 70; pl. 11).

Each of the grooves *aq* had lodged a structure with no direct equivalent in recent Cyclostomes, yet it seems, nevertheless, very probable that this cavity was not occupied by any gill-lamellae but formed a duct or tube leading the water outwards to the external efferent duct of the gill-pouch, which was partly lodged in the groove *dext.* It seems also probable that the external duct was situated in the antero-median part of the external groove, and that the postero-lateral impression *dexta* which evidently was well supplied with (arterial) vessels probably was occupied by a quite different structure, about the real nature of which I have, however, no opinion.

The groove *pbg* is at first inspection easily taken for the groove for an efferent branchial artery (cf. Stensiö 1932, pl. 25:1) but on closer examination we find that it differs in several respects from the grooves for efferent arteries (to be described later on). It is thus not situated in close connection to an interbranchial or, more correctly in this case, to a corresponding prebranchial ridge, it does not reach on to the aorta groove or even as far medially as to the aorta ridge, it has no side-branches, and it is (in its median part) traversed by narrow grooves which must have lodged arteries as they run on to and end on the ventral part of the aorta ridge (cf. below). As the groove cannot possibly have lodged any efferent artery, I am inclined to think that it possibly gave passage to a structure corresponding to that (vertical) part of the peripharyngeal (ciliated) groove in the larva of *Petromyzon* which is a rather deep and conspicuous structure, running in the lateral pharyngeal wall on to the roof of the pharynx immediately in front of the anterior (hyoidean) gill-sac (cf. Schneider 1879, p. 84; Dohrn 1885, figs. 15, 17; 1887, pl. 4; Willey 1894, pp. 168—169; Schaffer 1895a, pp. 703—704; figs. 5—6; 1895b, pp. 310—312; fig. 23; Gaskell 1898, pl. 3:2; 1908, fig. 63; Reese 1902, pp. 92—94; fig. 5b—d; Goodrich 1909, fig. 37; Salkind 1915, pp. 301—302; Wallin 1917, pp. 137—143; fig. 2—3; Daniel 1931, p. 44; fig. 2; Leach 1939, p. 564). According to Dohrn (1885, pp. 54—55; figs. 15, 17; 1887, pp. 309—314, 318—319; 1888, pp. 234—243) the peripharyngeal groove in *Petromyzon* has, however, arisen by a transformation of the first pair of visceral pouches (corresponding to the first pair of supposed gill-sacs in the Cephalaspids), and if this conception is correct then the interpretation of the groove *pbg* as having lodged the peripharyngeal groove apparently loses its foundation. v. Kupffer (1895) and particularly Goette (1901, pp. 540—543) contest the point of Dohrn, and Goette considers the vertical part of the groove to be related only to the anterior wall of the pouch, and Damas (1943, pp. 225—227) who has carried out the most recent investigation in this matter, has in the main confirmed the view of Goette with regard to the vertical portion of the peripharyngeal groove (he says, p. 273, that the groove is formed by the anterior third of the epithelium of the first visceral pouch). Be that as it may with regard to the ontogenetic facts, it seems nevertheless, evident that the peripharyngeal groove is a very ancient structure phylogenetically, inherited from the pre-vertebrate ancestors, and that once it must have been present when a spiracular gill-pouch was wholly developed. Later, with the disappearance of this pouch, it must have shifted backwards to its present position in front of the anterior (morphologically second) gill-sac.

However, we must not entirely disregard another attempt at a quite different interpretation of the groove *pbg,* viz. that it was the groove for a strongly developed vein in the roof of the branchial chamber, corresponding to the v. mandibularis in *Petromyzon.*

This vein in *Petromyzon* is a large vessel (in some species sinus-like, cf. Daniel 1934, "hyoidean sinus") which issues ventrally from the v. jugularis inferior (v. superficialis longitudinalis ventralis) and passes upwards in the wall of the pharynx, medially to the ascending subotical part of the ventro-lateral plate of muco-cartilage, following closely the course of the paripharyngeal groove and dorsally passing over into a longitudinal vein, commonly (but wrongly, Gelderen 1924; cf. Cori 1906; Hatta 1922; de Beer 1924; etc.) regarded as the v. cardinalis anterior (v. capitis medialis). Now this vein is said by Hatta (1922, p. 104) to arise from the primitive embryonic mandibular vascular arch which should have lost its connection with the truncus arteriosus and obtained a new one with the "v. cardinalis anterior". If this be true, the groove *pbg* cannot be the groove for a corresponding vein as the spiracular gill-sac was well developed and its vascular arch in front of it must be assumed to have been normally functional though the efferent division (at least in *C. signata)* was rather rudimentary (cf. below). The ontogenetic history of the v. mandibularis is, however, not wholly clear as the description by de Beer (1924, pp. 324—327) of the conditions of the vein system in a young larva of *Petromyzon* is incompatible with the statements of Hatta, and, according to the former, the v. mandibularis has nothing to do with the differentiation of the mandibular vascular arch. Under these conditions it is, of course, impossible to form an opinion as to the possible presence of a corresponding vessel in the fossil Osteostraci.

With regard to the impressions th_1—th_3 it may be noticed that they are cavities in the ventro-lateral part of the roof of the branchial fossae, lying anteriorly to the external grooves, and that they thus are "segmentally" disposed, that the bottom of the impressions is uneven, and in some places crossed by vein canals (as will be seen later on). It can thus i. a. be supposed that the structures which were lodged in them were in some way related to the gills. By comparison with recent Cyclostomes we find dorsally and ventrally to the vestibule of each gill-sac in *Petromyzon* in the Ammocoetes stage nodular structures with granular surface, partly (the dorsal nodule dorso-laterally, the ventral nodule ventro-laterally) enclosed in a capsule of connective tissue, and lying near to the vv. superficiales longitudinales. Each of these structures closely resembles thymus rudiments in fishes and have been regarded as a glandula thymus or an incipient gl. thymus (Schaffer 1894; 1906, p. 67; Castellaneta 1913; Salkind 1915, pp. 297—304; cf. Keibel 1925, pp. 19—20; Pietschmann 1934, p. 382; Rauther 1937b, pp. 272—273; Damas 1943, p. 226). Judging from the shape and disposition of the cavities th_1—th_3 in the Cephalaspids, I find it rather probable that each of them really lodged a structure corresponding to the thymus or thymus-like organ or, more exactly, to the dorsal part of this organ in the *Petromyzon*-larva, and if this be so, it is of interest to note that these structures which in *Petromyzon* are rather small and evidently wholly disappear during the metamorphosis, in the Cephalaspids were large and well developed in the adults. In this connection it can be observed that the true gl. thymus in fishes arises as rudiments from the visceral pouches (but here from the most dorsal part of them) and takes an epibranchial position along the jugular vein (Dohrn 1884, pp. 141—151; Maurer 1886, pp. 149—159; Beard

1902; Hammar 1912, pp. 144—149, 167—171; Deanesly 1927; Hill 1935; Rauther 1937a, pp. 706—708; 1937b, pp. 273—275; etc.).

To judge from the disposition of the impressions of the branchial apparatus it seems obvious that this apparatus was developed in many ways as in the larva of the Petromyzonts, in as far as the gill-sacs most probably opened directly into the pharynx (as they also do in the Myxinids) without the formation of a sub-oesophageal, branchial tube as in the adult Petromyzonts. From the disposition of the canals for the afferent and efferent branchial arteries in the roof of the oralo-branchial chamber and thus along the lateral wall of the gill region (see below, p. 140), compared with the conditions of these vessels in the gill-sacs of recent Cyclostomes, it can furthermore possibly be inferred that the gill-sacs were not very deep, and that their epitrematic or dorsal parts were much more developed than their hypotrematic or ventral parts, and that they thus were more developed along the roof of the oralo-branchial chamber than near its floor. The pharynx has then probably been very wide and the gill-sacs not so closed and well circumscribed as in recent Cyclostomes (cf. Goodrich 1931). If the other interpretations put forward above represent the real facts we find that the Cephalaspids in several respects agree more with the Ammocoetes larva of the Petromyzonts than with the adult form in which i.a. the peripharyngeal groove and the thymus-like organ have disappeared. In the structure of the anterior part of the gill region the Ammocoetes larva is on the whole more primitively organized than the adult *Petromyzon* (cf. e. g. Balabaj 1935b).

We shall now return to the cast of the oralo-branchial chamber in *C. signata* for a consideration in detail of the grooves for different vessels and nerves, here present.

A pair of short longitudinal grooves *(arostr)* in the buccal area possibly represents the grooves for the paired rostral artery (cf. *Kiaeraspis,* Stensiö 1927, pp. 149—150, 206—207). The groove on the right side has a short median branch, and leads anteriorly to an opening into the ventral rim.

Before the velar ridge there are one or two very short transverse grooves on the side of the aortal ridge. Behind the velar ridge three distinct pairs of small narrow grooves *(ard, asp)* are seen coming from near the edge of the aortal ridge and running in dorso-lateral direction on the side of this ridge to the roof of the oralo-branchial chamber in the vicinity of the ridge; the first (anterior) and the third (posterior) of them branch rather frequently. The posterior pair *(asp)* of these grooves will be considered more closely. The groove *asp* on the right side of the shield sends out a small bifurcated branch in antero-dorso-lateral direction and runs then first in dorso-lateral direction. Just behind the inner end of the groove *pbg* it turns antero-ventro-laterally, running between this groove and the transverse series of pits *(igl),* and ends on the antero-lateral side of the third pit *igl;* it sends i. a. out one branch on each side of the second pit. The groove *asp* on the left side evidently (though the basal connection has not been directly observed) sends out a comparatively strong branch in antero-dorso-lateral direction, and runs after that dorso-laterally over the most dorso-median part of the groove *pbg* and then crosses the two first pits *igl* in the middle of their length.

On the border-line between the first and the second branchial fossae runs a groove *(aeff*$_1$*)* for the first efferent branchial artery (cf. Stensiö 1927, pp. 150, 174) which medially could be traced up to the lateral side of the aortal groove. The groove is fairly distinct as a main groove down to the ventro-lateral parts of the two fossae; it does not bifurcate but receives several small and often indistinct side-branches, mainly from in front. Some of these anterior grooves run in mainly postero-median direction in order to reach the main groove, others, however, run in mainly postero-lateral direction; one of these grooves *(aaff?)* crosses the most dorso-median part of the groove *aq*$_1$, and turns then in lateral direction, approaching the groove *aeff*$_1$ but is obliterated before reaching it.

Also the groove for the second efferent branchial artery *(aeff*$_2$*)* runs as a main groove between two adjacent branchial fossae, here the second and the third. It receives some side-branches from in front which are short and which could not be traced distally beyond the groove *aq*$_2$*;* two side-branches from behind are fairly long; they bifurcate in their distal end on the ridges *gl* in the third branchial fossa. The groove *aeff*$_2$ receives from behind the grooves for the n. facialis and in the middle of its length for a distance coincides with the groove for one of the branches of this nerve; the groove is in this place distinctly wider than medially and distally from there. In such cases it is, of course, very difficult to ascertain which of the side-branches of the groove had lodged a vessel and which had lodged a nerve, and there is thus a possibility that a groove which I interpret as a nerve groove really gave passage to an artery and vice versa; this reservation is valid also for the interpretation of some of the grooves between the third and the fourth branchial fossae. The groove *aeff*$_2$ is seen to be a double structure just medially to the point where it receives the groove for the n. facialis from behind, a low ridge partly cutting off a small anterior section which narrows medially. Laterally to the place where the anterior branches for the n. facialis leave the main groove, this latter (here lettered *aaff)* continues farther ventro-laterally and is here a well developed groove, and distally becomes even slightly broader; from behind it receives two small grooves *(aa)* which run in antero-ventro-lateral direction in order to join the main groove.

The groove for the third efferent branchial artery (*aeff*$_3$) runs between the third and the fourth branchial fossae. It is distinct in its median passage just in front of the otical prominence but farther distally it receives, or is crossed by, grooves for the n. glossopharyngeus and here the conditions are rather obscure. The groove *aeff*$_3$, however, receives some small arterial grooves from in front, two of them in front of the otical prominence, and two grooves from behind. As stated above (p. 93) the canal for the a. communicans (or the common canal for the a. communicans and the n. glossopharyngeus) opens into the oralo-branchial chamber at the groove for the a. branchialis efferens 3; more exactly, just behind the groove *aeff*$_3$ the canal in question passes over into a partly closed groove which communicates with the groove *aeff*$_3$. The groove *IX* + *acom* is in front of the groove *aeff*$_3$ continued by a longitudinal groove (*a* + *IXa*) and it is distinctly seen that this groove is a composite groove (as its roof is partly provided with a median longitudinal ridge), and thus the groove must have lodged two structures (one of them was a branch of the n. glossopharyngeus, the other an efferent arteriole).

The groove *aeff*$_4$ for the a. branchialis efferens 4 is only preserved in its most median part; it lies between the fourth and fifth branchial fossae and runs in dorso-median direction up to an opening in the anterior side of the canal for the a. subclavia (cf. fig. 11B). It will be further considered below in connection with the posterior efferent branchial arteries which are most conveniently treated separately after the description of the posterior part of the oralo-branchial chamber exposed in a specimen of *C. exilis.*

The grooves *aeff*$_1$—*aeff*$_4$ must have lodged the first to fourth efferent branchial arteries and of these the first to third must have joined the aorta directly, while the fourth one first joined the a. subclavia, lying behind it (whether the common trunk thus formed, the a. efferens communis par, emptied into the aorta or into an unpaired a. efferens communis could not be ascertained as the median parts of the postbranchial wall with the canals or grooves for them are not preserved in the specimen examined). As pointed out by Stensiö 1927, p. 175) these arteries must each have arisen from the arterioles in the gills of a branchial bar and thus from the adjacent halves of two subsequent gill-sacs, just as in *Petromyzon.* It is, however, remarkable that the efferent branchial arteries in the Cephalaspids lay so closely to the roof of the oralo-branchial chamber that they left impressions in this wall. In *Petromyzon* they are situated near to the median side of the gill-sacs, along the free ends of the branchial septa, running in almost dorsal direction to the aorta and thus far away from the branchial bars; parts of the gill musculature and the afferent branchial arteries lie in fact between them and the branchial arches (Julin 1887,

p. 777; pl. 21:3; Nestler 1890, pp. 18—20; pl. 6; Goette 1901, p. 543; figs. 24—26, 30—31; Cori 1906, p. 29; pl. 3:14; Gaskell 1898, fig. 2; 1908, fig. 71; Goodrich 1909, figs. 35, 37; Daniel 1934, pp. 320—325; figs. 4, 9; Rauther 1937b, fig. 196; cf. Hatta 1922, figs. 168—170; etc.). It can furthermore be observed that the efferent branchial arteries in the Cephalaspids ran as a main trunk (at least in that part of the gill region which has left imperssions in the roof of the oralo-branchial chamber) receiveing from in front and from behind small side-branches from the gills, and that they thus were developed as the corresponding arteries in the larva of *Petromyzon* (cf., besides the authors, just mentioned, Tretjakoff 1927b, pp. 220—221, fig. 1; cf. also the restorations by Stensiö 1927, figs. 41, 44, which, probably incorrectly, show the efferent branchial arteries bifurcating in the ventro-lateral part of the branchial fossae). The grooves joining the grooves for the efferent branchial arteries are, however, not regularly disposed as could be expected if they really gave passage to branches of these arteries but this fact can probably be explained by the assumption that the arterioles only occasionally lay in such a way that they caused impressions in the face of the endoskeleton. We can also note that the lateral extent of the grooves for the efferent branchial arteries was not inversely related to the median extent of the gill-sacs, as is evidently the opinion of Stensiö (1927, p. 175).

As stated above, some small grooves run in mainly postero-lateral direction towards the groove for the efferent branchial artery, as e. g. the grooves lettered *aaff?* and *aa*. These grooves can hardly be interpreted as having given passage to efferent arterioles; they possibly lodged afferent arterioles to the afferent branchial artery which, to judge from the conditions in *Petromyzon,* was probably situated closely to the efferent branchial artery in the same gill-septum. The conditions in the complex of grooves between the second and third branchial fossae can only be explained if we assume that the lateral part of the groove which is lettered *aaff* really lodged the afferent branchial artery of this branchial arch; then the anterior section in the groove $aeff_2$, just medially to the union of this groove and the groove for the n. facialis, must have lodged a median part of this artery. The two small grooves *(aa)* joining the groove *aaff* from behind have given passage to afferent arterioles.

The groove *asp* gave passage to an artery which probably was the dwarfed and transformed and posteriorly displaced original first efferent branchial artery; it is here called the a. spiracularis, and the groove *asp* the groove for the a. spiracularis.

The efferent branchial arteries form the dorsal aorta, and the anterior point of the aorta were thus the place of union of the first pair of efferent branchial arteries somewhat in front of the transverse level through the anterior end of the endocranium. The aorta was, however, continued in anterior direction by a nutrient artery. This artery was certainly an unpaired structure in its posterior part and passed along the aortal ridge which forms a direct continuation anteriorly of the groove for the dorsal aorta. The term aortal ridge (and aortal groove) is thus correct only for that part of the ridge (and groove) which, when present, lies posteriorly to a level with the origin of the grooves *asp,* but it will, nevertheless, be used for the sake of convenience also for the anterior continuation of the ridge (groove) and thus for the entire ridge (and groove). The artery which formed the anterior continuation of the dorsal aorta will be called the rostral artery (a. rostralis). It thus ran forwards on the aortal ridge from a point, anteriorly to the opening into the aorta of the a. spiracularis, as an unpaired vessel, and between this and the velar ridge gave off at least two pairs of side-branches (which were lodged in the grooves *ard)* to the dorso-median part of the roof of the first branchial fossa in front of the gills. Farther anteriorly it gave off minute branches on both sides of the ridge and then divided, forming the paired rostral arteries (in the grooves *arostr).*

Turning now to the grooves (and canals) for veins, we find anteriorly on the left side in the distal continuation of the velar ridge two rather large openings *(vr, vmarg)* in the ventral rim. The antero-median one *(vr)* of these openings is continued straight backwards by a distinct groove which, however, soon disappears at the anterior end of the first branchial fossa. The postero-lateral opening *(vmarg)* is continued by a fairly short groove which runs in postero-median direction to the point where the other groove ends; the two grooves thus join at an acute angle. On the right side of the shield which is somewhat fractured only the opening *vr* is observed (pl. 30:1). The foramen *vr* is the opening of the canal for the rostral vein (or rostral vein sinus, cf. Stensiö 1927, pp. 186, 226) and the foramen *vmarg* that of the canal for the v. marginalis (cf. Stensiö 1927, pp. 184—186, 227). The longitudinal groove running from the opening *vr* probably lodged the anterior continuation of the v. jugularis inferior ("v. superficialis longitudinalis ventralis", Stensiö 1927, p. 227, cf. p. 185; with regard to the corresponding vein in *Petromyzon,* cf. Nestler 1890, p. 22; Vialleton 1903, pp. 307—308, 324—325; Cori 1906, p. 58; fig. 3; Favaro 1908, p. 402; Mozejko 1910, pp. 622—625, 640; Hatta 1922, pp. 195—196; Daniel 1934, p. 329; fig. 8) and the short lateral groove contained the antero-median continuation of the v. marginalis or, expressed in other words, the v. jugularis inferior (which in the anterior part of the head was a paired vessel) divides anteriorly, giving on the one side rise to the v. rostralis which first ran in a groove on the ventral side of the ventral rim and then entered the most rostral part of the visceral endoskeleton through the opening *vr,* and on the other side communicating with the v. marginalis. It will be noted that in this species the v. marginalis and the v. rostralis for the most part went in closed canals, and not in open grooves.

In the posterior part of the buccal area there is a richly ramified system of fine grooves *(vbp)* which converge in a point in the postero-lateral part of the area where they abruptly disappear; some of the grooves begin on the side of the aortal ridge and some in the most anterior part of the first branchial fossa. These grooves most certainly lodged small vein branches, which drained the anterior part of the roof of the oralo-branchial chamber, and emptied into a short basal trunk which discharged into the v. jugularis inferior. They were branches of a vein which will be called the bucco-pharyngeal vein (v. bucco-pharyngealis). There are no correspondent veins in recent Cyclostomes and fishes as the roof of the mouth and the anterior part of the pharynx in these animals is drained by veins belonging to the epibranchial vein system (v. cardinalis anterior, cf. i. a. Hatta 1922, p. 143; Daniel & Bennett 1931).

In the middle of the ventro-lateral part of the first to fourth branchial fossa some grooves *(vnbr)* are interpreted as grooves for veins. In the second fossa a few grooves run in ventro-lateral direction, converge and join into a common main groove which ends on the median side of the impression th_2; anteriorly to this groove a short groove with three branches is seen which could not be traced far distally. The impression th_2 is, as mentioned above, traversed by a longitudinal groove with many side-branches. In the third fossa the grooves *vnbr* are more ramified than in the second fossa; here three main grooves converge in a point at the lateral margin of the cavity th_3 and to this point runs also a small bifurcated groove in the roof of this cavity. In the fourth branchial fossa only the median part of the groove *vnbr* is preserved. In the first branchial fossa on the left side of the shield only a single groove runs down to the median margin of the impression th_1, and on the ventro-lateral side of this impression a mainly longitudinal bifurcated groove is found; on the right side three grooves, each with a few side-branches, run separately in ventro-lateral direction towards the median margin of the cavity th_1.

The grooves *vnbr* are here considered to have lodged veins which drained the ventro-lateral part of the roof of the gill-sacs and emptied into ventro-median side-branches to the v. marginalis (the supposed transversal veins between the v. marginalis and the v. jugularis inferior, cf. Stensiö 1927, pp. 184, 226) or joined the paired v. jugularis inferior. These veins are here termed the vv. nutritiae branchiales (cf. the conditions in fishes, Parker 1887, p. 173; Allen 1905, p. 91; Daniel 1922, pp. 207—208; Marples 1936b, p. 830; etc.; in *Petro-*

myzon, Cori 1906, p. 58; Grosser 1907, p. 101; Favaro 1908, pp. 400—401; Mozejko 1910, p. 622; Hatta 1922, pp. 196—198; Daniel 1934, p. 329; in *Myxine,* Grodzinski 1926, p. 131; fig. 11). It is to be noted that these veins were closely associated with veins from the glandulae thymi (or thymus-like organs) or even received vein-branches from these organs.

Finally the grooves in the roof of the oralo-branchial chamber, supposed to have carried nerve branches, remain to be considered. Within the distal part of its passage through the visceral endoskeleton the canal for the r. maxillaris trigemini (V_2) divides on each side of the shield into three canal branches which open separately into the oralo-branchial chamber. The openings of the canals on the right side are continued in anterior or antero-lateral direction by distinct grooves in the roof of the oralo-branchial chamber. The two median canals open just on the groove *pbg,* and the groove (V_2a) from the most median opening is very narrow and runs for a short distance in anterior and very slightly median direction. The groove (V_2b) from the second opening is by far the largest; it runs in anterior direction but soon splits into two narrow, slightly diverging grooves. In the anterior continuation of the large groove most antero-ventrally in the roof of the chamber near the ventral rim, an opening (pl. 30:1, V_2b) is found just medially to the opening *vr,* and to judge from the conditions on the left side (see below), this is the opening of a canal for a superficial branch of the r. maxillaris. The lateral branch of the canal V_2 opens into the oralo-branchial chamber slightly behind the opening of the large canal just mentioned, and is continued for a short distance in antero-ventro-lateral direction by a narrow groove (V_2d) in the roof of the foremost part of the first branchial fossa. Just distally to the origin of this groove a short canal issues from the groove and runs through the posterior raised border of the groove *pbg* in order to open in the oralo-branchial chamber just in front of this border, and from this opening a narrow groove (V_2c) runs forwards almost parallelly to the large groove V_2b, bifurcating distally. Similar conditions prevail also on the left side of the shield; the grooves corresponding to the grooves V_2c and V_2d run, however, quite independently of each other, and the groove corresponding to the groove V_2a is here a median branch to the groove V_2b. The groove V_2b is continued forwardly by a canal in the endoskeleton through the velar ridge (pl. 30:1; cf. *Nectaspis,* p. 156). This canal opens anteriorly to this ridge and is followod by a groove, lying just medially to the groove from the opening *vr,* and this groove, in its turn, terminates at the opening of a canal in the ventral rim. One of the nerve branches of the r. maxillaris had thus pierced the roof of the oralo-branchial chamber just before the first gill-pouch, had continued in a groove in the roof of this chamber, had pierced the velar ridge, and finally entered the visceral endoskeleton in order to reach the superficial tissues of the most rostral part of the shield; it contained somatic sensory fibres. The other branches and grooves V_2 most probably gave passage to motor nerve fibres to the oral and pharyngeal and thus possibly also to (some) velar muscles, and to sensory fibres from the epithelium in the mouth and the anterior part of the pharynx (cf. *Petromyzon,* Fürbringer 1875, pp. 63—66; figs. 21—23; Johnston 1905a, pp. 155—156; pl. 5; Tretjakoff 1927a, pp. 387—390, 394—396; figs. 8, 10—12; Cords 1929, pp. 223—225; figs. 2, 3—4; Holmgren & Stensiö 1936, p. 279; Lindström 1949, pp. 371—374, 378—384; figs. 24, 27, 29—31).

The canal for the r. mandibularis trigemini (V_3) during its passage through the visceral endoskeleton divides into two branches which open into the oralo-branchial chamber in the anterior half of the second branchial fossa. From the median opening a very short groove runs in anterior direction and divides into two diverging branch grooves, a lateral and a median one, which run on to the groove $aeff_1$. Anteriorly to this groove the median groove has a narrow continuation (V_3a), running in antero-ventral direction in the roof of the first branchial fossa. In the distal continuation of the lateral groove, in front of the groove $aeff_1$, there is proximally a main groove which breaks up into several distal branches. Two of them (V_3b) are considered to have carried nerve fibres. One groove runs in antero-ventral direction and partly crosses the first branchial fossa, the other travels in antero-ventro-lateral direction obliquely across the groove aq_1. On the left side of the shield a corresponding groove (no other grooves of the r. mandibularis are preserved) divides distally into three branches of which one turns in medial direction over the branchial fossa 1 and two reach down over the depression th_1. The lateral opening of the canal V_3 is continued by a ventro-laterally running groove (V_3c) which can be traced to near the first interbranchial ridge.

The r. mandibularis trigemini which was transmitted by the canals and grooves V_3 was, as said above (pp. 65, 69), exclusively a motor nerve (the sensory fibres possibly associated with it proximally are assumed all to have been composed of general cutaneous or lateralis elements, coming from the trigeminus-lateralis chamber, and to have rather soon left the main trunk and run to the skin). The r. mandibularis, as far as can be judged from the course of the grooves V_3, innervated muscles in the first gill-pouch (and most probably also other, deep lying pharyngeal or ventral muscles). In this connection it must be pointed out emphatically that only some of the branches of a nerve lay so closely to the roof of the branchial chamber that they could leave traces in the endoskeleton, and that we do not know anything of those branches which undoubtedly must have turned ventrally or deeper into the soft tissues after they had pierced the roof of the oralo-branchial chamber; this reservation is, of course, also valid with regard to the following branchial nerves. In *Petromyzon* the r. mandibularis V innervates most of the intricate lingual musculature, some velar muscles and also some other deep muscles (cf. Fürbringer 1875, pp. 66—67; Johnston 1905a, pp. 153—154; Tretjakoff 1927a, pp. 392—393; Cords 1929, p. 225; Lindström 1949, pp. 369—371, 376—378), and in the Myxinids the motor trunk of the n. trigeminus innervates the very complex "tongue" musculature (cf. Allis 1903a, pp. 274—276; Lindström 1949, pp. 346—353), and as the musculature of the rostral part of the head in recent Cyclostomes is most probably much transformed secondarily in relation to the conditions in the Cephalaspids, no comparisons between the corresponding nerves can be made.

The canal for the n. facialis *(VII)* opens into the oralo-branchial chamber by a single opening (pl. 29:2, *VII)* dorsally in the third branchial fossa about midway between the second and the third interbranchial ridge. It is continued in antero-ventro-lateral direction by a very short groove which divides into two grooves. The median one of these grooves is rather broad and reaches on to the groove $aeff_2$, which here is fairly wide. From the anterior side of this widened part issue two grooves, and from its lateral continuation, the groove *aaff*, one groove arises, which I suppose had lodged nerve branches. The median groove *(VIIa)* runs in antero-dorso-lateral direction over the groove aq_2 and on to the anterior part of the branchial fossa, its distal end lying just postero-medially to the opening of the median canal for the r. mandibularis trigemini. The nerve groove *(VIIb)* next to it in the lateral sense crosses the same groove and, at the anterior margin of it, divides into three narrow grooves, two short median ones and a rather long lateral indistinct one. This latter groove turns over in ventro-lateral direction and crosses two of the ridges *gl*. The groove *VIIc* issues from the median part of the groove *aaff* and runs in ventro-lateral and somewhat anterior direction over the groove aq_2 and bifurcates; it ends at the median margin of the fossa th_2. The lateral groove *VIId*, arisen from the bifurcating groove *VII*, is narrower than the median one; it runs in antero-ventro-lateral direction on to the groove *aaff* which it meets somewhat ventro-laterally to the origin of the groove *VIIc*.

The branchial rami of the n. facialis must thus have innervated mainly structures in the second gill-pouch, between the first and second interbranchial ridges or in the region morphologically in front of the second gill-opening, just as is the case in modern Petromyzonts (Alcock 1898, pp. 140—143; pl. 2:1-2; Johnston 1905a, pp. 161—162; pl. 5; 1908, p. 576; figs. 7—8, 19; Tretjakoff 1927a, pp. 403—404; Cords 1929, pp. 231—232; fig. 4; Holmgren & Stensiö 1936, pp. 279—280;

Lindström 1949, pp. 386—387, 390—391). Whether a median branch of the nerve (passing in the groove *VIIa*) contained visceral sensory fibres (and thus was a r. visceralis) or not, cannot be decided with any certainty (cf. Stensiö 1927, pp. 159—162, 165, 194) but, to judge from the conditions in *Petromyzon,* it seems very probable that such fibres were present, even if they were not collected into a special visceral branch (cf. Fusari 1907; Johnston 1908, pp. 586—591).

As said above in connection with the intracranial passage of the n. glossopharyngeus, its canal (or, more exactly, the common canal for the n. glossopharyngeus and the a. communicans) opens into the oralobranchial chamber, on the right side of the shield, immediately behind the third interbranchial ridge just on the groove for the third a. branchialis efferens. This is the main glossopharyngeal canal opening, but slightly before the canal opens, it must have given off a short lateral canal which opens slightly laterally to the main canal opening. The grooves for the branches of the n. glossopharyngeus issuing from the anterior side of the composite groove $aeff_3$ are intermingled with arterial grooves but the following grooves are supposed to have given passage to nerve branches. As mentioned above (p. 140) the groove $a+IXa$ is a composite groove and had lodged an efferent arteriole and a branch of the n. glossopharyngeus. Laterally to the exit of this groove the groove $aeff_3$ has a distinct swelling, and from this widened part of the groove issue i. a. two grooves for nerves. The median one *(IXb)* of them runs in antero-ventro-lateral direction over the groove aq_3 and gradually turns over into a ventro-lateral direction in the middle of the third branchial fossa. The other groove *(IXc)* which issues slightly laterally to the median one and is narrower than this runs mainly in ventro-lateral direction along the roof of the groove aq_3 and divides into several fine branches. The groove *IXd* issues from the opening of the lateral glossopharyngeal canal and runs in ventro-lateral and slightly anterior direction on to the groove $aeff_3$ which it joins somewhat ventro-laterally to the exit of the groove *IXc*. On the left side of the shield the canal for the n. glossopharyngeus (the branchial ramus) divides, as said before (p. 93), during its passage through the endoskeleton, and the canal branches open into the oralobranchial chamber by foramina of their own and apart from the arterial grooves. We thus find that the grooves for the branchial rami of the n. glossopharyngeus are directly comparable with those of the n. facialis (as here interpreted), and it is thus very probable that the branchial rami of both these nerves were developed in the same way. To judge from the grooves of the n. glossopharyngeus this nerve innervated (mainly) the third gill-pouch or the region between the second and the third interbranchial ridge or that which morphologically lay between the second and third gill-openings (cf. *Petromyzon,* Alcock 1898, pp. 144—146; pl. 2:1, Johnston 1905a, pp. 169—172; figs. 17—18; pl. 5; 1908, pp. 573—574, 576—577; figs. 5—10; Tretjakoff 1927a, pp. 408—409; Cords 1929, p. 235; fig. 4).

The canals and grooves for the branches of the n. vagus will be considered below after the description of the posterior branchial fossae, preserved in a specimen of *C. exilis*. In pl. 27:1 is shown a rather complete cast of the oralo-branchial chamber in *C. exilis*, and here we find conditions somewhat different from those just described in *C. signata*.

In the anterior part of the shield the visceral endoskeleton was considerably thinner than in *C. signata* and did not reach sufficiently far downwards for the branchial apparatus to leave such impressions as in this species. The interbranchial ridges are very feebly developed, and the most prominent sculpture is produced by ridges caused by the canals V_2 and sel_1 (pV_2, *psel;* cf. also pl. 9:6).

In the branchial fossae 1—4 (k_1—k_4) the ventro-lateral parts are well defined, and the external grooves *(dext)* are well developed and deep. The antero-ventro-lateral part of the fossae forms a rounded depression and corresponds possibly to the depression *th* in *C. signata*. The transverse canals *(v)* from the canal *vmarg* or *vsmarg* enter the antero-lateral sides of the external grooves of the fossae 1—5 but farther backwards these canals descend into the space between the outermost parts of two subsequent fossae.

The openings of the canals for the r. mandibularis V (V_3) are seen in the antero-ventro-lateral part of the first fossa, those of the n. facialis *(VII)* in the second fossa, those of the n. glossopharyngeus *(IX)* and the a. communicans somewhat laterally to the middle of the third fossa, and those of the first branchial ramus of the n. vagus just postero-laterally to the otical prominence in the fourth fossa.

The aortal groove is strongly developed; it reaches forward to a transverse level through the middle of the first branchial fossa or to the origin of the groove *asp;* before this point the sharp-edged aortal ridge is seen running forward. Somewhat behind the origin of the canal for the internal carotid *(acar)* the groove sends out a pair of large side-grooves ($aeff_2$) for the second efferent branchial arteries, which are, however, soon obliterated; the right one receives from behind two small grooves. Somewhat anteriorly to the exit of the canal *acar* a pair of grooves ($aeff_1$), smaller than the grooves $aeff_2$, are sent off from the aortal groove, they are the grooves for the first efferent branchial arteries; still more forward another pair of fairly small grooves *(asp)* are given off, which are caused by the a. spiracularis. Anteriorly a narrow canal *(arostr)* is seen running from the aortal ridge in mainly lateral direction. It ends on the postero-lateral corner of the buccal area, and as seen in a specimen of *C. retusa* (pl. 9:6) and as mentioned below (p. 154), just at the opening of a branch from the most anterior part of the canal for the a. marginalis. In the lateral part of the third interbranchial ridge there is on the left side of the shield a narrow groove *(aaff?)* and on the right side two adjacent very narrow grooves; the former groove is seen gradually to taper in median direction; possibly this groove as well as one of the grooves on the right side had lodged the distal part of an afferent branchial artery.

Having accounted for the anterior part of the oralo-branchial chamber and the four anterior branchial fossae $(k_1—k_4)$ which are well developed and rather large, we now turn to the posterior branchial fossae. The fifth fossa (k_5) forms a transition to the four posterior ones which are very narrow, and form long and deep grooves; the last fossa (k_9) is, however, somewhat broader and indistinctly bounded medially. The fifth fossa is in its major part disposed transversely to the main axis of the shield, its distal fourth turning abruptly in postero-ventral and slightly lateral direction. The branchial fossae 6 and 7 (k_6, k_7) are in their inner half directed laterally and slightly posteriorly from the median line while their outer half is bent in posterior and somewhat lateral direction. The fossae 8 and 9 (k_8, k_9) are in the main (in the distal two-thirds of the length) disposed almost parallelly to the main axis of the shield. It can be observed that medially to the outer part of the fossa 9 there is a short and shallow fossa or groove (k_x) with an almost transverse disposition (cf. Stensiö 1927, fig. 39).

The canal for the a. subclavia *(asubcl;* in this species the artery was wholly enclosed in a canal in the endoskeleton), coming from the zonal endoskeleton, traverses the distal part of the branchial fossa 5 and then runs dorsally to the interbranchial ridge 5 and, more medially, dorsally to the branchial fossa 6. Somewhat medially to the posterior bend of the fossa 5 the canal has an opening on its antero-ventral side $(aeff_5)$ which is most probably the opening for the a. branchialis efferens 5 (cf. Stensiö 1927, pls. 107:F 30; 108:F 31, $a. eff_6p$). Further medially, in its dorso-median part, the canal *asubcl* receives from behind a rather large and short canal which opens on the postero-ventral side of the canal. This canal *(afc)* is formed by the union of three canals from the dorso-median part of the postbranchial wall, more precisely, the canal *afc* sends out a lateral branch $(aeff_6)$ and then, almost immediately, divides into two canals $(aeff_7$ and $aeff_8)$. The lateral canal $aeff_6$ can be traced in distal direction to the antero-dorsal side of the branchial fossa 7 near the interbranchial ridge 6, in which fossa it opens. The canal $aeff_7$ is short and runs to the antero-dorsal side of the branchial fossa 8, and the canal $aeff_8$ which is much longer runs to the distal half of the fossa 9, where it opens in its lateral part. In the dorsal side of the branchial fossa 5 there is an opening $(aeff_4)$

just postero-medially to the opening for the first branchial ramus of the v. vagus, and this, to judge from the conditions in *C. signata,* must be the anterior opening of the canal for the a. branchialis efferens 4 which joined and opened into the canal *asubcl* on its antero-dorsal side, about opposite to the opening of the canal *afc.* Part of this canal corresponds to the posterior of the two canals in *C. hoeli,* lettered "Xbr_2—Xbr_6" by Stensiö (1927, figs. 33—34, cf. fig. 39). From the junction with these efferent branchial canals ($aeff_4$—$aeff_8$) onwards (in median direction) the canal *asubcl* will now be called the canal *aeffcp* (see also pl. 9:7) or the canal for the paired common efferent artery (a. branchialis efferens communis par); it passes on to and opens into the unpaired canal *aeffc* or the canal for the a. branchialis efferens communis impar, which in this species is slightly asymmetrically disposed as its posterior part is turned somewhat to the left from the median line. It must be noted that the canals for the paired a. efferens communis join the canal *aeffc* somewhat before its posterior end, and furthermore that this latter canal is open posteriorly, in other words, that it traverses the post-branchial wall and opens into the trunk cavity (pl. 27:1); this is also the case in *Axinaspis* (pl. 99:2; cf. also Stensiö 1927, pls. 46:1; 47:1; 58). It is thus evident that the canal *aeffc* cannot have been traversed exclusively by an efferent artery but that in its posterior part it must have lodged an artery of a different nature. Very probably this was one or several nutrient arteries for structures in the trunk, possibly corresponding to the paired artery for the pronephros or the unpaired a. intestinalis anterior or the a. mesenterica in *Petromyzon* (Julin 1887, pp. 789—791; pls. 21:2; 22:2; Favaro 1908, pp. 378—380; Hatta 1922, pp. 150—152, 162—163) or the a. coeliaca in the Myxinids (Jackson 1901, p. 26; fig. 18; Cole 1925, p. 312; fig. 1; Grodzinski 1926, p. 144; cf. also the conditions in *C. hoeli,* Stensiö 1927, figs. 35, 39; pl. 107, and in *Boreaspis,* p. 163).

We shall now return to the specimen of *C. signata,* examined before, and consider what is preserved of the arterial and nerve canals and grooves connected with the posterior gill-pouches. In the chapter on the occipital region of the endocranium we have accounted for the proximal parts of the canals for the vagus branches and the arterial canals developed in connection with them.

It will first be noted that on the left side of the shield the canal for the first branchial ramus of the n. vagus is found to pierce the roof of the oralo-branchial chamber and to open into the proximal part of the groove for the fourth efferent branchial artery, and that this groove leads on to an opening in the a. subclavia (cf. fig. 11B; pl. 31:5-6). The a. branchialis efferens 4 had thus opened into the a. subclavia and not into the a. branchialis efferens communis impar or the aorta.

On the right side of this specimen of *C. signata* the canal for the subclavia *(asubcl,* pl. 29:2-3) is preserved in its entire length. It is seen that the canal runs in antero-median direction from the zonal endoskeleton in to the visceral endoskeleton in the subclavian ridge; the canal then turns and ascends in antero-dorso-median direction in the postbranchial wall, lying closely to the posterior side of this wall. Coming to about a level with the postero-lateral corner of the labyrinth cavity the canal turns again rather abruptly over into a median and slightly ventral direction and opens on the posterior side of the postbranchial wall, on which it is continued for some distance by a groove. The canal sends out numerous small ramifying ventral canals *(apw)* to the postbranchial wall. Just at the dorsal bend of the canal *asubcl* it has an opening on its anterior side ($aeff_4$, cf. fig. 11B), being the opening of a very short canal, running in antero-lateral direction and piercing the roof of the oralo-branchial chamber just at the fourth interbranchial ridge (pl. 35:3, $aeff_4$). This is the canal for the a. branchialis efferens 4, which thus opened proximally into the a. subclavia. The canal is continued distally by a groove in which the canal for the r. branchialis 1 vagi (Xbr_1, pls. 29:2; 35:1; cf. fig. 11B) opens. An opening (Xbr_1a) into the antero-dorsal side of the canal Xbr_1 is probably the opening of a canal corresponding to the grooves *IXa* for a branch of the n. glossopharyngeus and *VIIa* for a branch of the n. facialis. It will be observed that the canal *asubcl* is somewhat larger distally to the opening $aeff_4$ than proximally to this point.

Somewhat medially to the foramen $aeff_4$ the canal *asubcl* (or more correctly the canal *aeffc*) receives from behind a branch from a canal for the n. vagus and sends out in ventral direction two very short canals (Xbr_{2-3}, $aeff_5$, pl. 29:3) which open on the posterior side of the postbranchial wall and are continued by two converging grooves. These join to form a common groove *(aX)* which immediately passes over into a canal which traverses the thin postbranchial wall and opens on the anterior side of the wall. One, probably the median one, of the two canals and the corresponding groove is the canal and groove for the a. branchialis efferens 5 ($aeff_5$) while the other, probably the lateral one, transmitted the second and third branchial rami of the n. vagus (Xbr_{2-3}). The common opening (a_1X in pls. 29:3; 35:3, which transmitted the a. branchialis efferens 5 and the r. branchialis 2 vagi) on the anterior side of the postbranchial wall is continued in lateral and slightly ventral direction by a groove ($aeff_5$, pl. 35:3) between the fifth and sixth branchial fossae, along the interbranchial ridge 5; it is the groove for the fifth efferent branchial artery.. Three grooves *(Xa, Xb, Xc,* pl. 35:3) running over the posterior part of the fifth branchial fossa correspond to the grooves *IXa, IXb, IXc* and *VIIa, VIIb, VIIc,* respectively, and contained branches of the second r. branchialis X. The groove *aX* just before it passes over into a canal, sends out a branch (*Xbr_3*, pl. 29:3) in ventro-median direction on the posterior side of the postbranchial wall which runs on to an opening. Another rather large groove (*afc*, pl. 29:3) is found running from the groove for the a. efferens communis (par) to the same opening. The common opening (a_2X, pl. 29:3) leads into a short canal through the postbranchial wall. During its passage the canal divides into two branches which open on the anterior side of the wall by a rather small dorso-median ($aeff_6$, pl. 35:3) and a somewhat larger ventro-lateral opening (afc_1, pl. 35:3), both lying straight ventrally to the common anterior opening of the canal transmitting the a. branchialis efferens 5 and the r. branchialis 2 vagi. To judge from the conditions in *C. exilis,* the common trunk for the three posterior efferent arteries (6—8) was lodged in the groove *afc*. During its passage through the postbranchial wall the trunk divided into two branches of which one, the a. branchialis efferens 6, went through the opening $aeff_6$, and the other, the common basal stem for the aa. branchiales efferentes 7—8, through the opening afc_1. In the groove Xbr_3 was lodged a branch of the n. vagus, presumably the r. branchialis 3 or possibly a branch containing the branchial rami 3 and 4.

We thus find that the aa. branchiales efferentes 4—6 must have opened separately into the a. subclavia or into the a. efferens communis par, as the median part of the artery is called, and that the r. branchialis 1 vagi was associated with the a. branchialis efferens 4, the r. branchialis 2 vagi with the a. branchialis efferens 5.

With regard to the posterior efferent branchial arteries and their canals (or grooves) we have found some facts which are not in agreement with the picture of their disposition given by Stensiö (1927, pp. 175—180). These facts are, however, obtained from a rather scanty and in some respects imperfectly preserved material, and in order to get a clear and complete idea of the conditions in question we must await an opportunity of studying better preserved specimens; Stensiö's material was also imperfect, consisting mainly of an incomplete specimen of *C. hoeli,* used for his series F of sections (Stensiö 1927, figs. 33—35, 39—40; pls. 106—112). According to Stensiö (1927, pp. 175—176) the aa. branchialis efferentes 3—5 (*"a. eff_4—a. eff_6"*) opened directly and separately into the a. efferens communis impar, while the three following efferent arteries joined the a. subclavia. The interpretation by Stensiö of the three pairs of foramina in the canal for the a. efferens communis (impar) as the openings for three pairs of efferent branchial arteries is, as is evident from the descriptions given above, not in accordance with my interpretations of the facts observed in *C. signata* and *C. exilis.* Since it is most improbable that the conditions were so variable within the genus that both our interpretations can be true, and as the facts related by Stensiö can be so interpreted that they harmonize with those here observed (see above), we must assume that the foramina in the canal for the a. efferens communis impar transmitted arteries other than efferent branchial arteries, and I think it rather probable that these arteries were nutrient arteries for the pharynx and possibly other structures in the oralo-branchial chamber (cf. *Petromyzon,* in which such arteries are issuing from the aorta, Favaro 1908, p. 375).

The canals and grooves for the marginal and rostral veins and arteries in some specimens of *Cephalaspis* will now be described.

In *C. signata* the wide canal for the v. marginalis *(v. marg)* is seen in pl. 29:2, and lateral to it, in cross-section, the canal for the a. marginalis *(amarg,* see also pl. 30:1). Anteriorly to the velar ridge the canal *vmarg* (pls. 29:2; 30:1) opens ventrally, and its opening is continued by a short groove in median and slightly posterior direction; it soon meets another groove which leads forward to the opening of the canal *vr* (for the rostral vein) as described above (p. 142).

In *C. exilis* (pl. 27:1) and *C. retusa* (pl. 9:6) we find somewhat different conditions. The canal for the v. marginalis *(vmarg)* issues from the marginal vein sinus *(vsmarg)* and runs forward in giving off transversal short median canals (v_3, v_2, for ventral transversal veins) to the external grooves of the branchial fossae 3 and 2 (k_3, k_2), and also numerous lateral branches to the canal *amarg*. More anteriorly it opens into the external groove of the first branchial fossa (k_1, cf. Stensiö 1927, pl. 110: F 45, *v. marg*, v_2, k_2). From the antero-lateral side of this groove issues another slightly curved canal ($vmarg_1$) and runs forward, opening into the oralo-branchial chamber near to the ventral rim, laterally to the branchial fossa 1 (this canal $vmarg_1$ corresponds to the posterior canal "*va*" in pl. 110, F 45, F 49 and to the anterior canal "*v. marg*" in pl. 109: F 39 and to the canal "*v. marg*" in pl. 109: F 42 and its anterior opening, lettered "v_1" in pl. 98 C 112, all in Stensiö 1927). The v. marginalis which was lodged in the canal *vmarg* passed through soft tissue in the postero-ventro-lateral part of the branchial fossa 1, then entered the canal $vmarg_1$, and anteriorly to this canal went in a groove along the ventral rim; anteriorly it opened into the rostral vein which in these species was enlarged to form a vein sinus *(vrs)*. This vein sinus was lodged in a large transverse groove in the anterior part of the buccal area (corresponding to the space, lettered "*dpr*" in Stensiö 1927, pl. 110: F 45, F 49). From this groove several canals issue in anterior or antero-ventral direction.

The canal for the a. marginalis *(amarg)* runs forwards from the zonal endoskeleton, lying laterally to the canal *vmarg*. During its forward progress it receives median branches from the canal *vmarg* and gives off numerous lateral branches; gradually it grows very narrow. The canal continues, however, in antero-median direction, and, anteriorly to the canal $vmarg_1$ has a few short median branches to the groove for the v. marginalis; most anteriorly it divides into a postero-median branch going to the groove *vrs* just at its lateral end near the end of the groove *arostr,* and an antero-median branch which soon joins an anterior canal from the rostral vein sinus; further medially it could not be followed (an anterior part of the canal *amarg* corresponds to the canal *"va"* in *Kiaeraspis* and *Hoelaspis* and to the anterior canal *"va"* in *C. hoeli,* Stensiö 1927, pls. 44; 55; 110: F 45). In these species the a. marginalis thus went in a canal of its own on to the rostral part of the shield and here very probably passed over into the transverse paired a. rostralis (which was a branch of the unpaired a. rostralis, the anterior continuation of the dorsal aorta). At the transition between this artery and the a. marginalis an antero-median branch was probably given off which i. a. gave origin to dorsal superficial arteries (such as those in the canals *ars* in other species).

We find thus that the v. marginalis and the v. rostralis in some species went wholly (or almost wholly) enclosed in canals in the visceral endoskeleton while in others they went partly enclosed in and partly outside, ventral to the endoskeleton. In the former case the anterior and antero-lateral parts of the roof of the oralo-branchial chamber are rather even but in the latter case it is provided with marked grooves and ridges, caused by impressions of these veins. These irregularities in the roof can be easily misinterpreted as impressions of the gill-apparatus with which they thus have nothing to do. (cf. Stensiö 1927, pls. 98—99, 109—110).

We shall now consider the conditions in the anterior part of the oralo-branchial chamber in *Nectaspis,* as it represents a type different from that just described in *Cephalaspis.* In this latter genus the oralo-branchial chamber forms a large and wholly continuous cavity in the antero-ventral part of the cephalic shield, separated posteriorly from the trunk cavity by the transverse postbranchial wall.

In *Nectaspis* (fig. 15C; pls. 106—109; 111) we find, however, that oralo-branchial chamber in *Nectaspis,* as it represents a type different compartments, a smaller anterior one and a larger posterior one. The anterior part of the oralo-branchial chamber is thus partly separated from the posterior one by a transverse ridge or partition reaching down from the roof of the chamber. As this partition does not reach down to the horizontal level of the ventral rim but ends dorsally to it, the two compartments are ventrally in open communication. Where the transverse separating wall laterally abuts against the lateral wall of the oralo-branchial chamber it is fairly broad and flat but in median direction soon becomes very thin and forms a sharp-edged ridge; it runs in median direction slightly backwards and near the median line of the shield becomes again rather broad. Its ventral side is here rounded. It cuts off the aortal ridge and the dorsal part of it forms the anterior limit of this ridge.

The transverse ridge or wall is regarded as forming the boundary between an anterior oral or buccal cavity and a posterior branchial cavity, and it will therefore be referred to as the velar ridge *(velr)*. It has been suggested by Stensiö (1927, p. 167) that, if a velum was present in the Cephalaspids it must have been formed by soft tissue projecting from "the interbranchial ridge 1", and as this ridge and the velar ridge in *Nectaspis* are corresponding structures, this assumption, in view of the conditions in *Nectaspis,* seems to be a most plausible one, and on this account the ridge in question is called the velar ridge.

The buccal cavity is rather shallow with its greatest depth posteriorly and postero-laterally. The postero-ventral margin of the ventral rim is smoothly rounded in its antero-median (rostral) part and passes rather gradually over into the roof of the buccal cavity. There is no indication whatever of the presence of any depressed area as in some other Cephalaspids (cf. Stensiö 1927, pp. 45—47, 150). The posterior part of the roof of the cavity is divided into a right and a left half by means of a low median ridge which, beginning from the anterior side of the velar ridge, reaches forwards about two-thirds of the length of the cavity; it can be regarded as an anterior continuation of the aortal ridge. The median ridge is fairly broad posteriorly but tapers gradually forwards and also gradually looses in height. Posteriorly, near the origin of the ridge, on its ventro-lateral sides there is a pair of openings *(arostr)* which must belong to canals corresponding to those for the rostral arteries in *Kiaeraspis* (Stensiö 1927, pp. 149—150, 205; figs. 4, 36; pl. 51).

In the lateral part of the roof of the buccal cavity, in the corner between the velar ridge and the ventral rim there is a rather distinct rounded fossa which antero-laterally is fairly well defined but which in medial direction passes over without distinct boundary into the rest of the dorsal wall of the buccal cavity; most laterally it reaches its greatest depth. The margin of the ventral rim, bordering the fossa ventro-laterally, is here sharp-edged. In the anterior wall of the fossa is the opening of the rostral vein sinus *(vrs)*. In the lateral wall of the fossa there are three foramina; an anterior smaller opening lies slightly more medially than the two posterior openings *(vmargl)* which are of uniform size and slightly larger than the anterior one. The anterior opening probably transmitted a branch from the a. marginalis or possibly the whole a. marginalis, and the two posterior ones probably lateral branches of the v. marginalis. The fossa is here given the noncommittal name the buccal fossa (fossa buccalis, *fb);* it corresponds to the ventro-lateral part of the fossa *"k_1"* in *Kiaeraspis* (Stensiö 1927, p. 151; figs. 4, 36; pl. 51) which by Stensiö is considered to be a (prespiracular) branchial fossa. From the descriptions of the rostral part of the oralo-branchial chamber in *Cephalaspis,* and in *Boreaspis* (see below, p. 158), it is quite clear that in these types there was no prespiracular branchial fossa, and from what will be said about the homologies in this part of the shield and with regard to the disposition of the nerve canals it is evident that the so-called first branchial fossa in *Kiaeraspis* and the corresponding buccal fossa in *Nectaspis* cannot have been a branchial fossa, lodging a prespiracular gill-sac, but that it must have had a quite different function. And as the fossa is present only in a few forms among the Cephalaspids but absent in others it is clear that the structure, which was enclosed in it, cannot have been a structure universally present in the Cephalaspids or of fundamental importance. But as to the real nature of it nothing definite can be said. There is a possibility that it was a muscle fossa for some strongly developed and transformed buccal muscles or that it lodged a buccal gland (it is well known that in *Petromyzon,* but only in the adult form, there is a pair of large buccal or "salivary" glands, Kaensche 1890, pp. 243—244; Haack 1903, pp. 114—120; figs. 1—8; Fahrenholz 1937, pp. 130—132; fig. 148; Damas 1935, pp. 178, 222; etc). The fossae (or more correctly the fossa *"k_1"* in Stensiö's description) are by Damas (1943, p. 233) tentatively compared with the prevelar invaginations of the stomodaeum in the *Petromyzon* larva (which, as shown by him, p. 217, are by no means branchial in nature) or to the apparatus connected with the hydrosinus in the adult lamprey (cf. Reynolds 1931). This latter assumption seems rather tempting; the stomodaeum would then possibly have been provided with diverticula, comparable to the hydrosinus, and their function would have been regulated by strong muscles (functionally comparable to the m. pharyngeus in *Petromyzon,* cf. also Tretjakoff 1926, pp. 296—297) which originated in the buccal fossa.

About midway between the median line of the shield and the ventral rim the velar ridge was traversed on each side by the r. maxillaris V. The canal for this nerve *(V_2)* pierces the roof of the oralo-branchial chamber in the middle of the first branchial fossa and is continued forward by a short groove in the roof of this chamber, which reaches to the posterior side of the velar ridge and ends at an opening for a short canal through this ridge. The canal divides and opens on the anterior side of the ridge with two foramina *(V_2a).*

The branchial cavity on each side is subdivided by the interbranchial ridges and septa into a series of compartments or fossae, the branchial fossae (Stensiö 1927, pp. 46, 150—154). In *Nectaspis* the interbranchial ridges are rather well developed in their lateral parts at the transition to the septa while most medially near the aortal ridge they are more indistinct and in their middle parts almost or, in some specimens, wholly obsolete. The anterior interbranchial ridges are slightly curved, and from their origin at the aortal ridge run in lateral and somewhat anterior direction; the ventro-lateral parts of the fossae lie thus somewhat more anteriorly than their dorso-median parts (contrary to what is the case in *Kiaeraspis,* Stensiö 1927, p. 151; figs. 4, 36; pl. 51).

The roof of the first fossa is pierced in its lateral third and somewhat in front of the first interbranchial ridge by the canal of the r. mandibularis V *(V_3).* This canal is from its opening continued forwards by two short diverging grooves, one running in anterior, the other in antero-lateral direction. The lateral wall of the fossa is pierced by three canals of which two open by fairly large foramina. One of these openings *(vmarg)* lies ventrally to the most postero-lateral part of the velar ridge and the other *(v_1)* in the most postero-ventro-lateral part of the fossa; between them there is the third imperfectly preserved opening. The opening *vmarg* is continued forward to the buccal fossa by an indistinct groove in the ventral side of the lateral part of the velar ridge. The v. marginalis thus went forwards in the canal *vmarg* and then in the groove on the velar ridge; in the lateral part of the buccal fossa it passed through soft tissue and probably joined the v. jugularis inferior and the v. rostralis (or the rostral vein sinus; cf. the conditions in *C. signata,* p. 142).

In the second fossa opens the canal for the n. facialis *(VII).* The lateral wall of this fossa has two openings, of which the posterior fairly large one *(v_2)* leads into a short canal opening into the canal for the v. marginalis; immediately in front of the median opening of the canal there is another much smaller opening. The openings v_1 and v_2 are the openings of canals for ventral transverse veins from the v. marginalis.

The second interbranchial ridge reaches the aortal ridge somewhat before the orbital prominence, at a transverse level with the middle division of the ethmoidal cavity of the endocranium.

The third interbranchial ridge abuts against the anterior part of the orbital prominence, and the fourth one runs in a direction towards the groove between this and the otic prominence (cf. pl. 111:3).

The aortal ridge is well developed and provided with a distinct aortal groove. From the aortal groove issues a groove *($aeff_1$,* for the a. branchialis efferens 1) running in lateral and slightly anterior direction on the here feebly marked interbranchial ridge 1. Anteriorly to this point the aortal groove sends out a lateral groove *(asp,* for the a. spiracularis) which slightly behind the velar ridge pierces the small ridge bordering the aortal groove, and which on the right side is seen to continue for a short distance in lateral direction in the anterior half of the first branchial fossa. The aortal groove disappears behind the velar ridge in giving rise to a pair of small grooves *(av)* running in antero-ventro-lateral direction on the posterior side of the velar ridge; the right one reaches on to an opening in this ridge near the median line; these small grooves possibly lodged nutrient arteries for the velum. In the anterior continuation of the main aortal groove a canal runs through the velar ridge, and this is the canal for the rostral artery. During its passage through the thick median part of the velar ridge the canal (probably) divides into two branches, each opening, as said above, anteriorly in the buccal cavity on the side of the median ridge.

In this connection can be mentioned that the postbranchial wall is exposed in several specimens (part of it is seen in pl. 113:2). It is perforated by the large opening for the oesophagus, and ventrally has a notch for the truncus arteriosus.

In *Boreaspis* the conditions with regard to the shape of the anterior part of the oralo-branchial chamber are quite different from those in *Nectaspis*.

In *Boreaspis* (fig. 15A; pls. 78:2-3; 85; 86:2; 87; 93—94; 95:1) we find as in *Cephalaspis* a continuous oralo-branchial chamber. The antero-median part of the ventral rim is very broad and its posterior margin is abruptly truncated forming the anterior transverse border of the oralo-branchial chamber. In *B. robusta* and *B. puella* it has been observed that the aortal ridge does not reach so far antero-ventrally as to abut against the ventral rim but ends somewhat behind it. The short gap between the anterior end of the aortal ridge and the postero-ventral margin of the ventral rim forms a narrow but fairly broad groove which in lateral direction becomes narrower than it is medially. The groove is thus broadly triangular in outline; the posterior border of the groove is raised so as to form a faintly marked transverse ridge (pls. 78:2; 87:2). It can be noted that the exoskeleton on the postero-ventral margin of the ventral rim is thickened and traversed by numerous minute canals (probably vascular canals, pl. 87:2). In view of the conditions in *C. exilis* and *C. retusa* it seems most probable that the groove in question in *Boreaspis* lodged the rostral vein sinus, and that it had nothing to do with so-called depressed area, the supra-oral field, in some Cephalaspids or the triangular tooth-bearing area in other Osteostraci (Stensiö 1927, pp. 45—46, 150; Kiær 1928, pp. 127—129; Stensiö 1932, p. 37; Heintz 1939, pp. 33, 81).

The first branchial fossa is very spacious, distinctly larger than each of the subsequent fossae. It is bounded posteriorly by a distinct transverse interbranchial ridge *(ibr*$_1$*)* which is almost straight or with

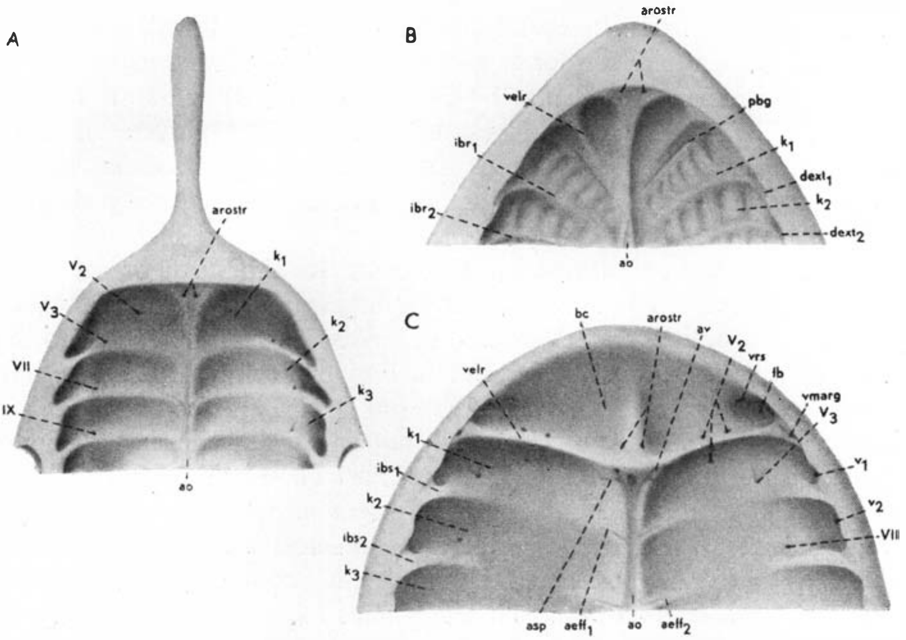

Fig. 15. — Anterior part of the oralo-branchial chamber of A, *Boreaspis costata,* B, *Cephalaspis acuminata,* and C, *Nectaspis areolata.* Ventral view. A and B, × 2, C × 3¾.

$aeff_1$—$aeff_2$, grooves for the first and second efferent branchial arteries; *ao,* aortal groove; *arostr,* canals for the a. rostralis; *asp,* groove for the a. spiracularis; *av,* groove for the a. velaris; *bc,* buccal cavity; $dext_1$— $dext_2$, grooves probably for the external efferent ducts from the first and second gill-sacs; *fb,* fossa buccalis; ibr_1—ibr_2, first and second interbranchial ridges; ibs_1—ibs_2, first and second interbranchial septa; k_1—k_3, first to third branchial fossae; *pbg,* groove probably for the peripharyngeal ciliated groove; *velr,* velar ridge; *vmarg,* canal (and groove) for the v. marginalis; *vrs,* canal for the rostral vein sinus; v_1—v_2, canals for the first and second ventral transversal veins; V_2, canals for the r. maxillaris V; V_3, canal (and grooves) for the r. mandibularis V; *VII,* canal for the n. facialis; *IX,* canal for the n. glossopharyngeus.

a slight anterior bend and directed laterally (fig. 15A; pls. 85; 86:2; 87:1) or laterally and somewhat anteriorly (pls. 93:1; 94:2); ventrolaterally it turns in postero-lateral direction and passes over into the first interbranchial septum. Forwards the first branchial fossa reaches on to the rostral end of the oralo-branchial chamber. As a whole this (and the three subsequent) branchial fossa forms a uniformly broad, in outline rectangular compartment in the oralo-branchial chamber, which only postero-laterally is curved somewhat backwards or the postero-lateral corner of which is somewhat protracted. In some *Boreaspis* specimens (e. g. of *B. robusta)* two divisions separated by a faint, low, rounded ridge *(velr?)* can be distinguished in the first branchial fossa, viz. a shallow, shelf-like anterior division and a slightly deeper posterior division (pl. 78:2-3).

The first interbranchial ridge in *B. costata* is provided medially with a distinct, and the second one with a rather indistinct transverse groove issuing from the aortal groove; these grooves were caused by the aa. branchiales efferentes 1—2, respectively. In other *Boreaspis* species the interbranchial ridges are indistinct or obsolete in their median parts but the grooves for the aa. branchiales efferentes in the roof of the oralo-branchial chamber are very well developed (pls. 93:1; 94).

The second to fourth branchial fossae are short and broad. The position of the anterior interbranchial ridges and the grooves for the anterior aa. branchiales efferentes in relation to other structures in the shield varies somewhat in different *Boreaspis* species. In *B. costata* the three anterior interbranchial ridges (ibr_1—ibr_3) lie entirely ahead of the orbital prominence, and the fourth one (ibr_4) abuts against the anterior half of this prominence (pls. 85; 86:2; 87:1). In *B. macrorhynchus* the third interbranchial ridge (ibr_3) runs in medial direction towards the anterior margin of the orbital prominence, and the fourth one (ibr_4) towards the posterior margin of this prominence; the groove for the fourth efferent branchial artery joins the aortal groove postero-medially to the orbit (pls. 93:1; 94, ibr_4, $aeff_4$). In *B. batoides* the grooves for the anterior aa. branchiales efferentes have a corresponding position (pl. 95:1).

In *B. costata* the anterior branchial fossae with exception of the first have shifted forwards as compared with those in *B. macrorhynchus* and *B. batoides* and encroached upon the first fossa; this fossa is thus comparatively smaller in *B. costata* than in *B. macrorhynchus* or *B. batoides*.

The anterior branchial fossae are uniformly shallow in the median two-thirds of their breadth (cf. however the first one, see above); in their lateral third they become suddenly considerably deeper and there is in fact formed in each of the four anterior fossae a distinct cavity in their lateral part (pls. 81:2; 93:1; 94:2). These cavities which will be called the branchial cavities are well displayed in a specimen of *B. robusta?* (pl. 81:2). Those in the second and third branchial fossae are best developed and consist here of a lengthened sigmoidally bent pit or groove; in the second fossa the anterior (and dorso-median) transversely rounded part (k_2a) of the cavity, which is rather deep, lies near to the first interbranchial septum (ibs_1). This part is continued in postero-lateral direction by a short, shallower part leading over into another deep part (k_2b, which is considerably narrower than the antero-median one) in front of the interbranchial septum 2 (ibs_2), and hence there is again a shallow groove (*dext*) running in postero-ventro-lateral direction, ending near the ventral rim. The branchial cavity can thus be said to consist of an anterior median (k_2a) and a posterior lateral (k_2b) pit, connected by a shallow groove and continued postero-ventro-laterally by another shallow rather long external groove *(dext)*. The cavity in the third branchial fossa is similarly built but the antero-median pit is much larger than in the second cavity; in the fourth fossa the antero-median pit is shallower than in the two other fossae and not so well defined. In the first branchial fossa the branchial cavity is on the whole smaller than the two following ones and the antero-median part is not so widened. Also the fifth (k_5), sixth (k_6), and seventh (k_7) cavities are seen in this specimen and lie on the anterior side of the lateral part of the postbranchial wall (cf. Stensiö 1927, p. 154). The fifth cavity consists of a very indistinct dorso-median part and a well marked external groove; of the sixth and seventh cavities only the external grooves are developed but two small indistinct pits in the antero-dorsal part of the postbranchial wall probably belong here though they are quite separated from their external grooves. No further cavities are present medially to the seventh one. In *B. macrorhynchus* (pls. 93:1; 94:2) four shallow impressions on the anterior side of the postbranchial wall represent the four hindmost branchial fossae (k_4—k_7); the three foremost fossae (k_1—k_3) are also seen.

The canals for the vv. transversales ventrales (cf. Stensiö 1927, pp. 183—185) open into the postero-lateral pit at the transition to the external groove (v_1—v_3); the fourth (v_4) opens, however, into the antero-lateral side of the external groove, and the following three canals (v_5—v_7) into the spaces between two adjacent grooves.

The roof of the first branchial fossa is pierced in its antero-lateral part by the canal for (a ventral branch of) the r. maxillaris V (V_2), and in its postero-lateral part somewhat before the interbranchial ridge 1 by the canal for the r. mandibularis V (V_3, pls. 78; 81:2; 85; 86:2; 87:1). In other specimens the opening of this latter canal lies closely behind the first interbranchial ridge (or the groove for the first efferent branchial artery). The opening of the canal V_3 is continued in anterior and slightly lateral and ventral direction by two slightly diverging grooves in the roof of the first branchial fossa (pls. 78:3; 83:2; 85; 93:1; 95:1) or by three such grooves (pl. 96). The canal for the n. facialis *(VII)* opens into the postero-lateral part of the second branchial fossa or closely behind the second interbranchial ridge (pls. 83:2; 85; 87:1; 91:1; 93; 94:2; 95:1); in some specimens two or three grooves from this opening are seen to cross the ridge (pls. 93:1; 94:2; 96). Into the postero-lateral part of the third fossa opens the canal for the n. glossopharyngeus (*IX*, pls. 85; 87:1; 93; 94:2; 95). In the specimen of *B. robusta?*, referred to above, the canal for the r. mandibularis V (or for a lateral branch of this nerve) opens into the oralo-branchial chamber medially to the antero-median pit in the second branchial fossa, slightly behind the interbranchial septum 1, and is continued by a groove running in antero-ventro-lateral direction to the antero-median pit in the first branchial fossa. The groove for the n. facialis runs forwards from the opening of the canal *VII* to the connecting part between the antero-median and the postero-lateral pit in the cavity k_2. The canal for the n. glossopharyngeus *(IX)* opens into the oralo-branchial chamber closely behind the antero-median pit in the cavity k_3.

The branchial cavities correspond to similarly shaped cavities in *Hoelaspis* (Stensiö 1927, pls. 44; 46:1) and to the deepened ventro-lateral thirds of the branchial fossae in *Kiaeraspis* (Stensiö 1927, figs. 4, 36; pl. 51) and *Cephalaspis exilis* and *C. retusa* (pls. 9:6; 27:1). Whether the branchial cavities in *Boreaspis* contained the dorsal part of the gill-sacs or only were impressions of the gl. thymus (or thymus-like organ) and the external ducts cannot be definitely ascertained. The disposition of the openings of the canals for the branchial nerves far laterally in the oralo-branchial chamber speaks for the assumption that the gill-apparatus in *Boreaspis* did not reach so far medially as in *Cephalaspis*. Be that as it may, the cavities, however, show us the number of the branchial fossae, and it is thus clear that in *Boreaspis* they were never more than seven. As to the number of the gill-sacs in the living forms, however, we cannot from this fact infer anything with certainty; there can possibly have been gill-sacs medially to the seventh branchial fossa which have not left any impressions in the anterior side of the postbranchial wall, but, on the other hand, there is a possibility that in *Boreaspis* not so many gill-sacs were formed as in *Cephalaspis.*

The first branchial fossa in *Boreaspis,* lying anteriorly to the first interbranchial ridge corresponds in *Nectaspis* to the first branchial fossa and the buccal cavity; the buccal cavity in this genus can possibly be regarded as to correspond to the anterior shallow part of the first branchial fossa, which is seen in *B. robusta* (and *B. costata).* The first branchial fossa in *Boreaspis* is thus also equivalent to the so-called "first" and "second branchial fossae" in *Kiaeraspis* (Stensiö 1927, figs. 4, 36; pl. 51, k_1, k_2), and the branchial cavity in the first branchial fossa in *Boreaspis* corresponds to the ventro-lateral part of the so-called "second branchial fossa" in *Kiaeraspis.* It is of great importance to note that in *Boreaspis* there is no cavity that can be compared with the buccal fossa in *Nectaspis* or with the ventro-lateral cavity in the so-called "first branchial fossa" in *Kiaeraspis,* and that *Boreaspis* has no real ridge corresponding to the velar ridge in *Nectaspis* (or *Cephalaspis)* or to the "interbranchial ridge 1" in *Kiaeraspis.* The first branchial fossa in *Boreaspis* certainly contained only the first gill-sac.

In the posterior part of the oralo-branchial chamber we meet some conditions different from those in *Cephalaspis* with regard to the canals for the efferent branchial arteries and some other arterial canals. We have mentioned previously that the a. branchialis efferens 4, in a groove along the fourth interbranchial ridge, joined the aorta. How the fifth efferent artery was disposed is unknown but at least in *B. costata* (cf. pl. 85) it seems beyond doubt that it must have emptied into the aorta. In *B. costata* (pls. 85; 86:2) the canal for the a. subclavia receives from behind and ventrally a canal *(afc)* which must correspond to the canal *afc* in *Cephalaspis* and *Kiaeraspis* (p. 149; pl. 97:3; cf. Stensiö 1927, p. 179, figs. 36, 39—40) in as far as it must have enclosed the two posterior efferent branchial arteries, here the sixth and seventh or, if the latter one was not developed, only the a. branchialis efferens 6. After the union of these canals the common canal (for the a. efferens communis par, *aeffc*) passes in median direction up to and unites directly with the aortal canal *(ao)*.

Thus in *Boreaspis* the paired a. efferens communis opened separately and directly into the aorta, while in *Cephalaspis* (and *Hoelaspis, Kiaeraspis, Axinaspis)* the paired a. efferens communis proximally ran, probably as a common trunk (the a. efferens communis impar) in a common unpaired canal before it opened into the aorta. The difference between the types is evidently of no great importance.

In *Boreaspis* the postbranchial wall is (as well known) perforated by the independent openings for the oesophagus and the truncus arteriosus, and in some species they are separated by a very narrow and delicate transversal skeletal bar (pls. 83; 88:4) but in others by a broader interval (pls. 84:2; 85).

In *B. costata* (pls. 85; 86:2) we now find an unpaired opening *(apn)* in the postbranchial wall just above the opening for the oesophagus, situated asymmetrically somewhat to the left of the median line, and in *B. macrorhynchus* (pl. 94:2) a canal *(apns,* or possibly only a groove in the posterior side of the postbranchial wall) is seen on the left side, opening into the ventro-lateral side of the aortal canal. It will also be noticed that in a corresponding place on the right side there is a short vertical groove *(apnd)* in the posterior face of the postbranchial wall which does not reach on to the aortal canal. The opening *apn* and the canal *apns* must have transmitted an artery coming from the trunk. In some species the artery passed through an opening in the postbranchial wall in order to reach the aorta but was in others lodged in a canal in this wall (or possibly only in a groove on the posterior side of it) and joined thus the aorta somewhat more backwards than in the other species. It is probable that the artery was paired but that the artery on the right side joined the aorta behind the postbranchial wall. If this be true, the artery possibly was an artery for the pronephros and not corresponding to the unpaired a. intestinalis anterior or the a. mesenterica in *Petromyzon* (cf. Julin 1887, pp. 789—

791; pls. 21:2; 22:2; Favaro 1908, pp. 378—380; Hatta 1922, pp. 150—152, 162—163). It can be observed that in *C. hoeli* a paired canal, having probably enclosed an artery for the pronephros, joins the canal for the a. afferens communis from behind (Stensiö 1927, p. 245; figs. 35, 39; pl. 107).

We shall now add some details related to the region of the oralobranchial chamber, observed in some other Cephalaspids in the present material. The specimens examined are often by no means so completely preserved or so instructive as those described above but are, nevertheless, in several respects of great interest and reveal structures which are of importance or which can be interpreted in the light of the more complete knowledge we have gained from a study of the better preserved material.

Conditions similar to those in *C. signata,* or more specifically, the buccal area, the groove *pbg,* the transverse series of pits *(igl)* in the first branchial fossa, have been observed in a few species, viz. *C. hastata* (pl. 36:2), *C. ibex* (pl. 38:1), *C. corystis* (pl. 33:2), all evidently closely related to *C. signata,* and in *C. kozlowskii.* Traces of the pits *igl* have been seen in *C. oreas,* and the groove *pbg* in *C. excellens* (pl. 13). The buccal area and velar ridge, similar to those in *C. signata,* as well as the branchial fossae with their external grooves, are seen in *C. crofti* (pl. 26:2), and the buccal area and the velar ridge are also observed in *C. exilis.* In *C. hoeli* the buccal area seems to be wholly confluent laterally with the first branchial fossa, and the velar ridge is thus not developed in the antero-lateral part of the oralobranchial chamber.

In *C. acuminata* (fig. 15B) in which the shield is anteriorly protracted and acuminated, the shape of the rostral part of the oralobranchial chamber is somewhat different from that in *C. signata.* The shape of the branchial fossae is on the whole as in this species but the anterior part of the first fossa is narrow since the velar ridge which is fairly distinct only in its antero-ventro-lateral part lies near to and parallel to the groove *pbg.* The aortal ridge is rather broad and provided with a distinct aortal groove posteriorly and forwards as far as to a transverse level with the first branchial fossa. Farther anteriorly it becomes sharp-edged but most forwards it again broadens and passes over into a triangular shelf which abuts against the ventral rim. In this shelf there is an indistinct groove which divides anteriorly into two grooves, each leading on to an opening *(arostr)* into the ventral rim. The grooves lodged the unpaired rostral artery which split into two branches and passed in a pair of canals in the most rostral part of the endoskeleton. Between the triangular shelf and the velar ridge the roof of the buccal area is excavated so as to form on each side a fairly deep depression; this cavity is deepest in its broad and rounded antero-ventral part but grows shallower and is finally effaced towards its narrow dorso-median part. Possibly this cavity was of the same nature as the buccal fossa in *Nectaspis* (p. 156).

In *C. ibex* (pl. 38:1) the interbranchial septa 1—6 are preserved, and it is of importance to notice that the septa on their median and ventro-median side are not provided with any perichondrial bone-lining. This means that the bone-layer which lines the septa on their anterior, posterior, and ventral sides can be followed only for a short distance in median direction before it ends abruptly. Similar conditions can also be observed in a specimen of *C. hoeli,* used by Stensiö for his series F of sections (Stensiö 1927, pls. 109—110). As this fact cannot be satisfactorily explained as a result of imperfect preservation, it can only mean that in the living animal the septa must have continued in unossified tissue farther medially than is evident from their fossil state. These unossified bars must thus have formed a median, or morphologically ventral and hypotrematic, continuation of the branchial arches of which the septa are a part. In other words, they formed part of the ventral visceral endoskeleton (cf. p. 116, and Stensiö 1927, p. 144).

The place of the openings into the oralo-branchial chamber of the nerve canals has been dealt with above (p. 124; cf. also p. 144); here shall only be mentioned that in *C. excellens* (pl. 13) the canal V_2 opens into the first branchial fossa about midway between the first interbranchial ridge and the groove *pbg,* and is continued in anterior direction by a groove which divides into two bifurcating branches, crossing the groove *pbg.* The canal V_3 of which the main trunk never reaches up to the outer face of the endoskeleton opens into the oralo-branchial chamber very far medially, on the right side of the shield in the holotype (pls. 13; 16:1) just before the second interbranchial ridge, and is here continued by two grooves, running in antero-lateral direction; on the left side the canal opens somewhat in front of this ridge and from the opening a groove can be followed in antero-lateral direction on to the first interbranchial ridge before it disappears (the opening of the canal V_3 into the oralo-branchial chamber is also seen in pl. 16:2).

In *Hoelaspis* the canal V_3 opens into the first branchial fossa and is continued in antero-ventro-lateral direction by a short groove (pl. 77:2; cf. Stensiö 1927, pls. 44—45). The canal *VII* opens into the oralo-branchial chamber at a point in the lateral continuation of the groove for the second efferent branchial artery or somewhat before this point in the second branchial fossa, and is continued in antero-ventro-lateral direction by a long (sometimes bifurcating) groove (pl. 77:2; cf. Stensiö 1927, pls. 44—45; 46:1; the groove *"VIIv"* is a groove in the roof of the oralo-branchial chamber closed towards the endoskeleton, and cannot have transmitted any branch of the n. facialis).

The conditions in the lateral parts of the oralo-branchial chamber of *Hoelaspis* (as seen in Stensiö 1927, pl. 44) are almost exactly as in *C. exilis* and *C. retusa.* The marginal vein ran in a canal *(v. marg)* which opens into the branchial fossa 1 *("k_2")* and then for a short distance in soft tissue in this fossa, and more forwards again in a canal which opens into the oralo-branchial chamber (at the point lettered "k_1"); the vein then traveled ventro-medially to the endeskeleton. Somewhat antero-medially to the point "k_1" there is a marked pit resembling a branchial fossa which possibly represents the place of union of the marginal and rostral veins into the v. jugularis inferior. The rostral vein sinus was lodged in a groove in the roof of the most anterior part of the oralo-branchial chamber (the canal *"vs.r"* is a superficial canal from this groove). The canal *"va"* transmitted an anterior part of the a. marginalis. The groove "$a.eff_1$" lodged a well developed a. spiracularis.

In *Benneviaspis* the anterior part of the roof of the oralo-branchial chamber is poorly known but is apparently developed much as in *Hoelaspis* (cf. Stensiö 1932, pl. 49:3); the velar ridge *(velr)* and the buccal area *(ba)* are seen in pl. 71:1.

The structure of the oralo-branchial chamber is unknown in the genera *Ectinaspis, Tegaspis* and *Securiaspis;* the rostral vein sinus is, however, observed in a specimen of the latter genus (pl. 61).

In *Axinaspis* the shape of the anterior part of the oralo-branchial chamber is almost unknown; the indistinctly developed velar ridge *(velr)* and the first and second interbranchial ridges (ibr_1, ibr_2) with well developed grooves for the efferent branchial arteries are seen in a distorted specimen (pl. 100:1). In another specimen of the same species the five hindmost branchial fossae are preserved (pl. 99:1). The canal for the a. subclavia in its ventro-lateral passage is found running dorsally to an interbranchial septum and, to judge from the conditions in *Cephalaspis* (cf. above, p. 149) and *Kiaeraspis* (cf. Stensiö 1927, figs. 33, 39; pl. 51), this septum must be the fifth from in front (ibs_5) and the fossa before it must be the fifth branchial fossa (k_5). Postero-medially to the interbranchial septum 5 there are three septa (ibs_6-ibs_8) and four fossae k_6-k_8, k_x). The interbranchial septa are very short and very low, and have the appearance of being damaged; they are thus not covered with a perichondrial bone-lining, and must have been much higher than now preserved or else have been continued by bars of unossified tissue (cf. *C. ibex,* p. 165). The interbranchial septum 5 is, however, somewhat higher than the others and distally turned in ventro-median direction. The septa are continued in postero-lateral direction by rather low, round-edged ridges, bordering the peripheral parts of the fossae, which here form external grooves. From the interbranchial septum 7 runs a rather high and distinct ridge *(roes)* first in antero-median and later in straight median direction to the upper margin of the common opening for the oesophagus and the truncus arteriosus *(oes+tr)*. By this ridge the two most posterior fossae become partly separated from the anterior ones. The last fossa *(k*x*)* is very different from the preceding narrow fossae; it is polygonal in outline, broadest postero-laterally with a rather high antero-median wall, separating it from the opening *oes+tr* and also with a rather high, sharp-edged, narrow postero-lateral wall. It is most probably, and at least in its major part, not a branchial fossa and lodged certainly not a complete gill-sac, but as to what structure it may have contained I have no opinion. The real branchial fossae have each a not very deep, but at least in the fossa 6, distinct pit or depression just behind the interbranchial septum. Possibly this pit corresponds to the impression *th* in *C. signata,* supposed to have lodged a gl. thymus (or thymus-like organ). A canal for the a. efferens communis impar and nutrient arteries for the trunk is present also in *Axinaspis (aeffc,* pl. 99:2).

With regard to the general structure of the oralo-branchial chamber in *Kiaeraspis* nothing of importance is shown in the specimens of the material now at hand. It is, however, well known through the investigation by Stensiö (1927). We can observe that the anterior part of the chamber reminds somewhat of that in *Nectaspis* in as far as there is formed a buccal fossa, but this fossa is not very deep and must have been occupied to a major part by the anterior portion of the v. marginalis; this vein emerged from the postero-lateral part of the fossa (cf. Stensiö 1927, pl. 51, v_1). It can furthermore be noticed that the fossa has none of the characteristics of the branchial fossae behind it. The velar ridge is feebly developed or absent. There are nine branchial fossae, as in *Cephalaspis.* As in *Axinaspis* the postbranchial wall has a large opening, common for the oesophagus and the truncus arteriosus (contrary to what is said by Stensiö 1927, p. 148; cf. pls. 51—52; 53:2-3; 58). A pair of canals or grooves in the anterior side of the postbranchial wall from the canal for the a. efferens communis impar (cf. Stensiö 1927, pl. 51, *a. eff. com)* probably transmitted nutrient arteries for the most posterior parts of the pharynx. The proximal part of the canal for the sixth efferent branchial artery $(aeff_6)$ and the common canal *(afc)* for the two hindmost aa. branchiales efferentes are exposed in the specimen figured in pl. 97:3 (cf. Stensiö 1927, fig. 36).

In this connection it shall again be noted that in *C. signata* the fourth efferent branchial artery emptied into the a. subclavia on its anterior side. This must also have been the case in a *Cephalaspis* sp., figured by Stensiö (1927, pls. 24:2; 28); the canal *"vz"* is the canal for the a. branchialis efferens 4, which has an opening, lettered "Xbr_1", into the oralo-branchial chamber together with a branch of the first

r. branchialis vagi; the lateral canal "Xbr_1" transmitted another branch of the same ramus.

In *Acrotomaspis instabilis* (pl. 102:1) the velar ridge *(velr)* is well developed and runs from a point near the antero-lateral corner of the shield, where it is fairly broad, in postero-dorso-median direction and must have reached the aortal ridge at a transverse level with the most anterior end of the naso-hypophyseal opening (which in this species is excessively enlarged); the velar ridges thus enclose a comparatively large and shallow triangular buccal cavity *(bc)*. The first and the second interbranchial ridges (ibr_1, ibr_2) are indistinct, the latter runs in dorso-median direction somewhat anteriorly to the orbit. The canal V_2 opens into the oralo-branchial chamber in the broad lateral part of the velar ridge, and the canal V_3 opens just before the first interbranchial ridge and thus into the first branchial fossa.

In *Acrotomaspis* sp. 1 the median part of the velar ridge meets the aortal ridge slightly more posteriorly than in *A. instabilis*.

In *A. trinodis* and *Acrotomaspis* sp. 2, being geologically young members of the genus, the velar ridge *(velr*, pls. 104:4; 105:2, 4) is also well developed; its dorso-median end lies here at a transverse level with the middle division of the naso-hypophyseal opening. From the development of these endoskeletal structures it seems as if the rostral part of the cephalic shield had not been subjected to any (great) reduction but that instead the antero-lateral corners of the shield had been protracted forwards, and that within the genus there is a tendency to shift the naso-hypophyseal opening and the orbits in an anterior direction.

In a specimen of *Didymaspis,* figured by Stensiö (1932, pl. 54:1-2). the branchial fossae are exposed, and a comparison between this specimen and the Spitsbergen Cephalaspids makes it wholly clear, that the branchial fossa, lettered "k_1", corresponds to the first branchial fossa as here defined, and to the fossa "k_2" in Stensiö's interpretations and restorations of *Cephalaspis* and *Kiaeraspis*.

After having described the conditions in the oralo-branchial chamber in different Cephalaspids we can make a summary and some general conclusions with regard to the general morphological structure of the anterior parts of this chamber and of the anterior visceral parts of the head in the Osteostraci.

We have thus found that the development of the anterior part of the oralo-branchial chamber is rather different in different Cephalaspids. In *Boreaspis* no velar ridge is developed and the buccal cavity and the first branchial fossa form on each side a combined anterior compartment in the oralo-branchial chamber, in which the buccal cavity can be recognized at most as a more shallow anterior shelf. In *Cephalaspis* the velar ridge is slightly developed, separating a buccal area from the large first branchial fossa; in this fossa the gill-apparatus occupied only the posterior half *(C. signata* and others). In *Nectaspis* the velar ridge is strongly developed and continuous with its fellow of the other side so that they both form a transverse wall, separating an anterior buccal cavity from the branchial chamber proper behind the ridge; the common buccal cavity is provided with a pair of distinct lateral fossae of unknown significance.

In *Cephalaspis* and *Hoelaspis* the second interbranchial ridge runs medially over the anterior part of the orbital prominence. In *Nectaspis* (and *Kiaeraspis*) two interbranchial ridges lie in front of this prominence, and in *Boreaspis* three interbranchial ridges are situated in front of it. Thus the preorbital part of the shield is somewhat protracted in *Boreaspis* in comparison with that of *Cephalaspis*, and the whole branchial apparatus has been shifted forwards.

The first interbranchial ridge is a dorsal part of the hyoidean visceral arch, and the velar ridge (if of any morphological significance) probably forms a dorsal part of the mandibular visceral arch. No equivalent to a supposed premandibular arch is found in the Cephalaspids. The branchial fossa in front of the first interbranchial ridge which is the most anterior branchial fossa has thus a spiracular, and the second one, between the first and the second interbranchial ridges, a hyoidean position. The gills were probably of a type most closely resembling those of recent Cyclostomes, as assumed by Stensiö (1927), and the spaces in which they were enclosed can thus be referred to as gill-sacs. There were developed in the Cephalaspids one spiracular (mandibular or hyo-mandibular) gill-sac, one hyoidean gill-sac, one glossopharyngeal gill-sac, etc. but there was no prespiracular gill-sac (cf. Stensiö 1927, pp. 166—167), and much less two prespiracular gill-sacs, as assumed by Westoll (1937, pp. 17—18) and Watson (1937, pp. 123—124; cf. Moy-Thomas 1939, p. 17).

In comparison with the recent Cyclostomes we may note that, while the branchial apparatus in these forms is displaced far backwards, it is shifted much forwards in the Osteostraci and that the posterior gill-sacs were small in the Osteostraci and crowded in the posterior part of the head. This seems hardly to be a primitive trait. As remarked by Damas (1943, pp. 266—268), the branchial sacs had by no means retained any segmental disposition (if such a disposition was ever established, cf. e. g. Kingsbury 1926).

The Osteostraci were thus more primitive than the modern Petromyzonts in as far as they had one more gill-sac and one more gill-opening in front than these animals, but the conditions in the Osteostraci were wholly in accord with those revealed in the ontogenetic development of *Petromyzon* (in which a rudiment of a spiracular visceral pouch is established but never develops into a gill-sac) and are in no way opposed to the general scheme of development of the anterior part of the head in Vertebrates (as would have been the case if there really had been a prespiracular gill-sac, as supposed by Stensiö 1927; cf. Scott 1882, p. 142; Koltzoff 1902, pp. 425—429, 518—519; Kingsbury 1926; Claydon 1938; Damas 1943, pp. 228—234).

The zonal endoskeleton or the endoskeletal shoulder-girdle.

The zonal endoskeleton or the endoskeletal shoulder-girdle is a paired part of the continuous endoskeletal component of the cephalic shield, in which it forms the postero-lateral parts. It consists of the endoskeleton of the cornua and the shoulder-girdle proper (Stensiö 1927, p. 231). Its relations to the endoskeletal component of the cephalic shield proper have been pointed out by Stensiö (1927, p. 231), and it can here be noted that it is also continuous dorso-medially with that part of the endoskeleton which I have called the inter-zonal endoskeleton (p. 55).

The main features of the endoskeletal shoulder-girdle were in great outlines made clear by Stensiö (1927), but several of the superficial vascular canals of the dorsal side were first described by Zych (1937).

The principal characters of the shoulder-girdle, with reference to its cavities and canals, will briefly be recapitulated (see Stensiö 1927, pp. 177—178, 183—185, 231—235; Zych 1937, pp. 72—76, 83—84).

In the antero-median part of the shoulder-girdle lies a division of a large cavity for the widened section of the marginal vein, the marginal vein sinus, and this cavity *(vsmarg)* opens anteriorly with a fairly narrow foramen, or passes gradually over into a wide canal *(vmarg)* for the marginal vein. Posteriorly the vein sinus opens with a foramen in the postbranchial wall into the trunk cavity of the cephalic shield. The part of the marginal vein sinus lying within the shoulder-girdle is here called the zonal part of the marginal vein sinus, and that part of it, which is supposed to have lain behind the postbranchial wall is referred to as the post-zonal part of the marginal vein sinus. Two short canals connect the trunk cavity with the pectoral sinus, viz. a dorso-median canal *(nz)* for a brachial nerve, and a ventro-medial canal *(vbr_2)* for a ventral brachial vein. The zonal part of the marginal vein sinus is connected with the pectoral sinus through a wide canal *(vbr_1)* for a brachial vein which opened in the dorso-lateral part of the sinus. A canal *(asubcl)* for the a. subclavia traverses the shoulder-girdle, postero-ventrally to the cavity *vsmarg,* and gives off a canal *(abr)* for an artery to the pectoral fin (a. brachialis) and, somewhat medially to the exit of this canal, a small branch *(avs)* for a superficial artery to the ventral side of the shoulder-girdle. Where the canal *asubcl* reaches the antero-medial part of the cornu, it branches into a postero-lateral canal *(ac)* for the a. cornualis and an antero-lateral canal *(amarg)* for the a. marginalis.

With the guidance of the statements by Zych (1937) and after having examined the specimen of *Cephalaspis kozlowskii* upon which they are based, I shall now give a short, introductory resumé of the superficial dorsal vascular canals of the zonal part proper (see fig. 16; this account differs in some respects and interpretations from that of Zych).

In the most antero-median part of the shoulder-girdle, at the transition to the cephalic shield proper, there is a canal *(*asc_1*)* which issues from the roof of the trunk cavity of the shield somewhat behind the lateral part of the postbranchial wall; when reaching the upper face of the endoskeleton the canal runs in anterior direction and crosses the canal sel_5. On the right side of the shield it continues in lateral direction in the region between the canals sel_4 and sel_5 as far as to the lateral sensory field. The corresponding canal on the left side *("a. sp.,* canal for the a. dorsalis lateralis superficialis posterior") is somewhat more elaborately developed. The canal is assumed to have lodged an artery, and the canal is here called the canal for the first scapular artery *(asc,* "a. brachialis superficialis dorsalis anterior", Zych). Slightly postero-laterally to the origin of this canal another canal *(*asc_2*)* runs from the lower face of the endoskeleton just behind the postbranchial wall. On the upper face of the endoskeletal shoulder-girdle it turns in lateral direction and divides into an anterior branch and a second branch which travels closely behind the canal sel_5 in a slightly postero-lateral direction to the antero-median part of the cornu; the whole canal is here called the canal for the second scapular artery *(*asc_2; it is by Zych denoted *"a. bsda*$_2$*"* and *"abs*c_2*"*, and the artery in its second branch is called "a. brachialis superficialis cornualis dorsalis"). Posteriorly to the exit of this canal, rather far behind it (on the left side) or near to it (on the right side) there is a fairly large canal *(*asc_3*)*, issuing from a canal *("a.nz")* which pierces the antero-median wall of the zonal part from the trunk cavity and opens in the pectoral sinus through the foramen *nz* (presumably homologous to the canal with the same lettering in Stensiö 1927). The canal asc_3 (the canal for the third scapular artery; "c. communis", Zych), after having reached the dorsal face of the endoskeleton, divides into two main branches. One (soon dividing into three small branches; canals for the "a. brachialis superficialis$_{1-3}$", Zych) runs in medial and posterior direction, the other mainly in lateral and postero-lateral direction along the very margin of the pectoral sinus (the artery in it is by Zych called "the a. brachialis superficialis cornualis").

The canals asc_1 and asc_2 were thought by Zych to have arisen from the canal of the a. subclavia, and the canal *"a. nz"* to have lodged an artery emanating from the dorsal aorta. It must, however, be noted that no connecting canals between the canal for the a. subclavia and the two canals in question have been observed, and, to judge from their origin in the endoskeleton behind the postbranchial wall and their position in relation to the canal *"a. nz"*, especially the relation of the origin of the canal asc_2 to the proximal part of the canal asc_3 on the right side of the shield, it seems very probable that the arterial vessels, lodged in them, all originated from one and the same segmental artery behind the a. subclavia (cf. p. 99).

The vein canals of the dorsal side of the zonal endoskeleton consist mainly of a big canal (*vsc;* corresponding to the canal for the "vena brachialis superficialis dorsalis communis" or "r. superficialis dorsalis v. brachialis" with its branches "r. superfic. dorsales v. brachialis$_{1-3}$" and "v. cornualis" or "ramus superficialis dorsalis cornualis v. brachialis", Zych), called here the canal for the scapular vein (v. scapularis). Its branches are situated on the zonal part proper antero-medially and anteriorly to the pectoral sinus and on the antero-median part of the cornu.

The canal *vsc* was thought by Zych to have lodged a tributary of the v. brachialis. The connection between the canals *vsc* and vbr_1 (or vbr_2) was, however, not seen; we can notice that the basal common trunk *vsc* runs in proximal direction postero-ventro-medially and thus not in the direction towards the canal for the dorsal v. brachialis (vbr_1); it seems very unlikely that it would be a branch of this canal, nor are there any indications as to a connection between it and the ventral brachial vein (vbr_2). If we now consider the conditions on the left side of the shield (cf. Zych 1937, pls. 3; 4:1) we find in the postero-median portion of the zonal part a short canal "a_1", running from the trunk cavity to the pectoral sinus where it opens ventrally to the opening in the dorsal part of the pectoral sinus of the canal *vsc* (Zych 1937, pl. 3, *v. bsdcom*) and somewhat postero-medially to the opening of the canal *"a. nz"*. From the opening of the canal "a_1" there runs a faintly marked groove in dorsal and somewhat lateral direction in the wall of the pectoral sinus towards the opening *"v. bsdcom";* connected with this groove are two very short and shallow grooves coming from behind, and from the opening *"v. bsdcom"* runs a short groove in antero-latero-ventral direction. We have thus a connection, very indistinct, it is true, between the canal "a_1" and the canal *vsc,* and we may assume that the vein from the dorsal side of the shoulder-girdle, contained in the canal *vsc,* continued in proximal direction in a groove on the postero-median vertical wall of the shoulder-girdle and traversed the short canal "a_1", and we can furthermore assume that this vein emptied into a posterior division of the marginal vein, which lay behind the postbranchial wall. On the right side of the specimen

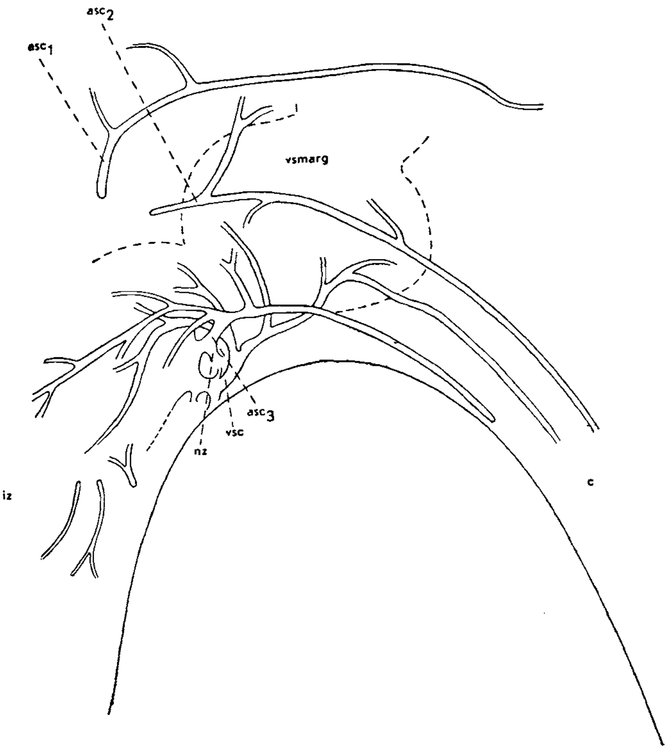

Fig. 16. — Diagram of the shoulder-girdle proper of *Cephalaspis kozlowskii,* with the superficial vascular canals and grooves (for the aa., vv. scapulares) restored. × 3.

*asc*1-3, canals for the aa. scapulares; *c,* cornu; *iz,* inter-zonal part of the cephalic shield; *nz,* canal for a nerve to the pectoral fin; *vsc,* canal for the v. scapularis; *vsmarg,* marginal vein sinus.

now considered, the direction of the canal *vsc* (Zych 1937, pl. 4:2, the left one of the canals lettered *"v. bsdcom")* is towards a depression in the postero-median vertical wall of the zonal part (lettered *"a. nz"* in Zych 1937, pl. 4:2) in which are two openings (as revealed by further preparation of the specimen) lying closely together, one, more median, corresponding to the opening *nz,* and the other to the opening of the canal "a_1", mentioned above. We find thus that the veins on the dorsal side of the shoulder-girdle proper (without any reasonable doubt) had no connection with the v. brachialis but that they, nevertheless, were tributaries of the marginal vein (sinus).

On the dorsal side of the most postero-median portion of the zonal part there are a few short canals of uncertain relations, probably lodging veins or arteries.

We have now tried to make clear the relations between the superficial vascular canals of the dorsal side of the shoulder-girdle proper in a well preserved *Cephalaspis* specimen and shall now turn to the Spitsbergen Cephalaspids. In the first place we shall consider a specimen of *C. vogti* in which the conditions are fairly simple and which furthermore supplements our knowledge of the vasular canals of the cornua, that is, the lateral parts of the shoulder-girdle.

In *C. vogti* (fig. 17; pls. 12:5; 18:1) we find no canals which can be interpreted as corresponding to the canals asc_1 and asc_2 in

C. kozlowskii; the function of the arteries lodged in them seems to have been at least partly (and in this specimen) taken over by dorso-lateral superficial arteries.

In the median part of the shoulder-girdle somewhat behind the foramen of the marginal vein sinus in the postbranchial wall (cf. pl. 18:1, *ov*) two openings are found, an anterior one *(asc)* and a posterior one *(vsc),* for two short canals ascending from the lower to the upper face of the zonal endoskeleton. Immediately laterally to the opening *asc* there runs a canal *(nz)* from the trunk cavity to the pectoral sinus, where it opens into the dorso-median part of the pectoral area; this canal evidently corresponds to the canal *nz* in *C. koslowskii* (fig. 16) and *C. exilis? ("C. hoeli",* Stensiö 1927, fig. 52; pls. 98—99) which very probably transmitted a nerve for the pectoral fin (Stensiö 1927, p. 233). The canals *asc* and *vsc* could be followed through the endoskeleton and were found, on the dorsal side of the endoskeleton, to form the scapular vascular canals (fig. 17; pl. 12:5; *asc, vsc),* the canal *vsc* corresponding to the canal with the same lettering in *C. kozlowskii,* the canal *asc* to the canal asc_3 in this species. Very soon after reaching the dorsal face of the endoskeleton the canal *vsc* divides into three branches, one running in antero-median direction, a second, rather small one, in anterior, and the third one (pl. 12:5, *vsc*) which is the largest of them, in antero-lateral direction. The canal *asc* branches into two canals running in opposite directions, one (pl. 12:5, *asc)* in median, the other in lateral and slightly posterior direction, just as in *C. kozlowskii.*

Most anteriorly in the pectoral sinus opens the wide and short canal for the v. brachialis (*vbr,* fig. 17; pl. 18:1), coming from the marginal vein sinus *(vsmarg);* on its lateral side it gives of a strong branch (figs. 5B; 17; pls. 12:5; 18:1, *vcm)* which runs in postero-lateral direction along the ventro-median side of the cornu, and which during its course gives off small branches *(vcos)* to the dorsal and ventral sides of the median part of the cornu. This branch *vcm* is here called the canal for the v. cornualis medialis, and is consequently thought to have lodged a vein which drained the median parts of the cornu.

From the canal of the v. marginalis or, more precisely, from the lateral side of the first widened part of this canal anteriorly to the marginal vein sinus, there issues a large canal *(vclat,* figs. 5B; 17; pl. 18:1) which first runs in postero-lateral direction crossing the canal *amarg* on the ventral side, and then in more straightly posterior direction on the ventro-lateral side of the cornu; it could be traced distally only to the middle of the length of the cornu, where it turns over and runs near the lateral margin of the cornu. This canal is called the canal for the v. cornualis lateralis, and contained a vein from the (antero-) lateral parts of the cornu.

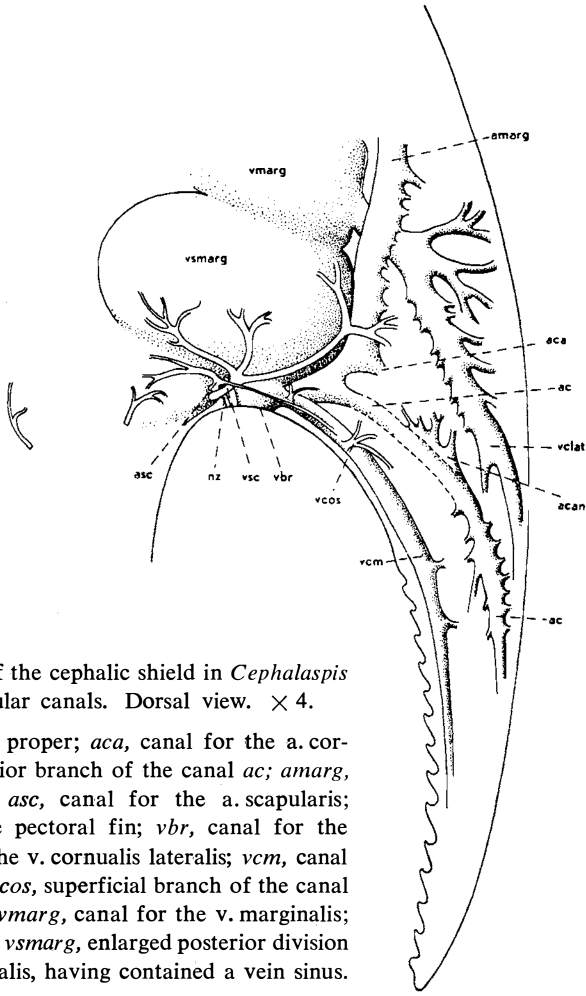

Fig. 17. — Right zonal part of the cephalic shield in *Cephalaspis vogti* with the principal vascular canals. Dorsal view. × 4.

ac, canal for the a. cornualis proper; *aca*, canal for the a. cornualis accessoria; *acant*, anterior branch of the canal *ac; amarg*, canal for the a. marginalis; *asc*, canal for the a. scapularis; *nz*, canal for a nerve to the pectoral fin; *vbr*, canal for the v. brachialis; *vclat*, canal for the v. cornualis lateralis; *vcm*, canal for the v. cornualis medialis; *vcos*, superficial branch of the canal for the v. cornualis medialis; *vmarg*, canal for the v. marginalis; *vsc*, canal for the v. scapularis; *vsmarg*, enlarged posterior division of the canal for the v. marginalis, having contained a vein sinus.

The canal for the a. subclavia branches in the usual manner postero-laterally to the wide marginal vein sinus into a canal for the a. marginalis and a canal for the a. cornualis proper. This canal *(ac*, figs. 5B; 17; pls. 12:5; 18:1), runs first in the central part of the cornu but in the anterior half of the cornu turns over to the lower face of the endoskeleton and runs along this face on the ventro-lateral side of the cornu. At the point where it reaches the lower face of the endoskeleton it receives an anterior branch *(acant*, fig. 17; pl. 18:1) from the anterior part of the lower side of the cornu. Soon after the branching of the canal *asubcl* into the canals *ac* and *amarg* the latter canal gives off a fairly strong branch *(aca*, fig. 17; pl. 18:1) which runs in the central part of the anterior half of the cornu in postero-lateral direction to the lateral margin of the cornu. The canal *aca* thus must have contained an artery for the antero-lateral part of the cornu, and is here called the canal for the a. cornualis accessoria. All the canals *vclat, ac* and *aca* give off numerous superficial branches.

On the postero-median part of the shoulder-girdle we find a small canal (and an additional one more medially to this canal and thus properly on the inter-zonal part of the shield; fig. 17); they are certainly vascular canals.

We can finally note that the anterior part of the shoulder-girdle is traversed by fine straight often undivided canals *n,* pl. 12:5) which very probably have lodged somatic sensory nerve fibres.

We shall now briefly consider some other Cephalaspids with regard to the superficial vascular canals of the shoulder-girdle and the variations in their disposition. These canals are, however, seldom well preserved or, when present, very difficult to analyze as to their course and nature; this is the cause why they, prior to Zych's investigation on *C. kozlowskii* (Zych 1937), had escaped attention or had not been dealt with.

The canals *vsc* or *asc* and their branches, apparently normally but more or less strongly developed, are seen in several *Cephalaspis* species as *C. excellens* (pls. 13; 14, *vsc), C. hyperboreus* (pl. 12:4; *asc, vsc), C. oreas* (pl. 8:2, *asc, vsc), C. divaricata* (pl. 6:2, *asc, vsc), C. verruculosa* (pl. 23:2, *vsc), C. hastata* (pl. 36:2, *vsc), C. doryphorus* (pl. 39:3, *vsc), C. sinuata* (pl. 23:1, *vsc)* and furthermore in *Benneviaspis holtedahli* (pls. 69:2; 70:1, *vsc)* and *Hoelaspis angulata* (pl. 77:2, *asc).* In *C. excellens* two separate canals for scapular arteries are seen in the holotype shield on its right side (pl. 13, asc_1, asc_2) and these canals were, as said above (p. 99) very probably connected with the canal and groove *asb* for a segmental artery (lying behind the occipital segmental artery); in *C. hastata* (pl. 36:2, asc_1, asc_2) there are also two similar canals of which the anterior one (asc_1) is strongly developed.

In *C. sinuata* (pl. 23:1) we find, laterally to the canal *vsc,* a branched superficial canal *(vcos)* which joins the canal *vcm* (described above in *C. vogti*); this canal *vcos* must have transmitted a superficial vein from the dorsal side of the transitional area between the shoulder-girdle proper and the cornu. In *C. oreas* two small canals (*vcos,* pl. 8:2) from the dorsal and dorso-lateral side of the shoulder-girdle proper are evidently of the same nature as the canal *vcos* in *C. sinuata,* and have joined the canal for the v. cornualis medialis.

In *C. ibex* (pls. 36:1; 37) the interrelations of the many superficial canals on the dorsal side of the shoulder-girdle are very confused, and several of them cannot be adequately interpreted. Two canals (asc_1?, asc_2?) are possibly canals for scapular arteries, two pairs of straight canals are interpreted as being nerve canals *(n),* and two rather small branching canals *(vsc)* near the pectoral sinus are most certainly branches of a common canal for a v. scapularis. As seen in pl. 28:2, the canals *vsc* are connected with each other by a groove in the dorsal part of the pectoral area which continues in median direction towards the canals *nz* and *vsc?*. Dorsally to the canal *vbr*$_1$ the groove is continued in ventro-lateral direction by a narrow groove which soon disappears; in this groove which is also seen in *C. signata* (pl. 30:2, to the right of the canal *vsc*) was certainly lodged a vein from the dorso-lateral part of the pectoral area. Laterally to the canals just mentioned in *C. ibex* there is a rather long canal *(vcos)* running in postero-lateral direction medially to the posterior part of the lateral sensory field; this canal very probably joined the canal *vcm,* and is here considered to have lodged a superficial tributary of the v. cornualis medialis. It drained partly the same area on the shield which in *C. hastata* (cf. pl. 36:2, *vsc)* was drained by the scapular vein.

In an undetermined *Cephalaspis* specimen (pls. 59:1; 60) we find a large number of canals, disposed in a confusing manner. The canal systems *vsc, asc* can be interpreted as corresponding to the canals *vsc* and *asc* in *C. vogti* and others, and an additional system of canals *(asc*$_1$*?)* possibly corresponds to the canal *asc*$_1$ and its branches in *C. kozlowskii.* The most conspicuous canal on the dorsal side of the shoulder-girdle is, however, a big longitudinal, sigmoidally bent vein canal *(vcom).* This canal is antero-dorso-medially connected with the system of dorso-lateral superficial vein canals *(vls),* and antero-laterally through the canal *vmsd* very probably with the marginal vein canal (cf. p. 123); posteriorly the canal joins the canal *vcm* (for the v. cornualis medialis). The canal *(vcom)* in question partly corresponds to the canal *vcos* in *C. sinuata* (pl. 23:1) and *C. ibex* (pls. 36:1; 37), and can be regarded as having lodged a dorsal superficial branch of the median cornual vein which had become enlarged and sinus-like.

We have thus found that the disposition of the superficial vascular canals on the dorsal side of the zonal endoskeleton is very variable in the genus *Cephalaspis,* and that this vascular system can be modified in different ways.

Besides in the genus *Cephalaspis* the superficial vascular canals of the dorsal side of the shoulder-girdle are very little known in the Spitsbergen Cephalaspids; *Benneviaspis* and *Hoelaspis* have been mentioned above; in *Nectaspis* (pl. 107) some canal fragments are seen but their course and interrelations could not be made out. In *Axinaspis* (pl. 99:2) a small canal *(vms)* is seen connecting the marginal vein sinus with the dorso-lateral face of the zonal endoskeleton.

The course of the vascular canals in the cornua is very poorly known in almost all the Spitsbergen Cephalaspids. The canal for the v. cornualis medialis *(vcm)* is seen in the pls. 28:2; 60 *(Cephalaspis)* and 71:2 *(Benneviaspis),* and the canal for the v. cornualis lateralis *(vclat)* in pl. 28:2 *(Cephalaspis)* and pl. 110:2 *(Nectaspis);* canals for superficial tributaries of the v. cornualis medialis are exposed in pls. 23:1; 28:2; 36:1; 37 *(Cephalaspis).* In *C. excellens* there are seen several transversal canals on the distal part of the right cornu, probably vein canals connecting the canals for the lateral and median cornual veins (pl. 13). In *Kiaeraspis* there are two canals (*ac, aca,* pl. 97:3) for cornual arteries (as in *C. vogti).*

In a specimen of *C. deltoides* some superficial vascular canals were observed on the ventral side of the shoulder-girdle but as it was impossible to get a clear picture of their disposition, they are not further considered here. In *C. ibex* (pl. 38:1, *vvs*) a canal pierces the postero-ventro-median part of the zonal endoskeleton, running from its ventral face to the trunk cavity, and probably giving passage to a superficial vein from the ventral side of the shoulder-girdle to the post-zonal part of the marginal vein sinus. In *C. signata* (pl. 29:2. *avs*) a canal from the canal *asubcl* (for the a. subclavia) leads into the marginal vein sinus, and is continued in antero-lateral direction by a short groove in the floor of this cavity to an opening in the floor. A branch of the a. subclavia had evidently run in this groove before it pierced the floor of the vein sinus and entered the ventral side of the shoulder-girdle, and this artery is comparable but not strictly corresponding to the r. superficialis ventralis of the a. subclavia in *C. hoeli* (cf. Stensiö 1927, pp. 177—178; fig. 40; pls. 109—112). In the same specimen a fragmentary vein canal was observed running in dorso-median direction through the ventral part of the zonal endoskeleton; its opening *(vvs)* into the marginal vein sinus is seen in pl. 29:2. Also in *Boreaspis costata* the opening *(vvs)* of two canals are seen in the ventral wall of the marginal vein sinus (pls. 85; 86:2); the anterior of them leads downwards into a canal which opens on the ventral side of the zonal endoskeleton. Most probably superficial veins from the ventral side of the shoulder-girdle went in canals through the endoskeleton in order to open into the marginal vein sinus through the foramina *vvs.*

We shall now consider the canals which pierce the pectoral area of the shoulder-girdle and which mostly contained vessels or nerves for the pectoral fin.

In a specimen of *C. ibex* (fig. 18; pl. 28:2) the pectoral area is fairly well preserved and we find here in its central part several large openings for different canals. The largest of them is the foramen for the v. brachialis proper *(vbr_1)* which lies laterally in this part and slightly nearer to the dorsal than to the ventral margin of the pectoral area; in *C. signata* the corresponding opening (pl. 30:2, *vbr)* is situated distinctly in the upper half of the pectoral area; the canal for the v. brachialis proper is also seen in *C. vogti* (as noted above; pl. 18:1, *vbr).*

Medially and somewhat ventrally to the foramen *vbr*$_1$ there is another opening *(abr),* the foramen for the main canal of the a. brachialis; the opening itself is directed obliquely, dorsally and medially, and is followed by a short but distinct groove in the pectoral area. As is seen in *C. signata* (pl. 30:2) the canal for the a. brachialis runs proximally near the lower face of the zonal endoskeleton. In approaching the pectoral sinus it turns in dorsal and median direction and opens in this species about midway between the dorsal and ventral margins of the pectoral area. The canal for the a. brachialis *(abr)* is also seen in *C. doryphorus,* connecting the canal *asubcl* with the pectoral sinus (pl. 40:3). Before it opens into the pectoral sinus the canal *abr* in *C. ibex* and *C. signata* gives off a small ventro-lateral branch which opens ventro-laterally to the opening of the main canal in the pectoral area (pls. 28:2; 30:2, *abr*$_1$).

Somewhat postero-medially to the foramen *abr* an additional big canal pierces the zonal endoskeleton and opens into the pectoral sinus (pl. 28:2, *vbr*$_2$); this canal (see also pl. 38:1, *vbr*$_2$) comes from the trunk cavity of the shield and pierces the zonal endoskeleton somewhat behind the subclavian ridge as is distinctly seen in *C. doryphorus* (pl. 40:3, *vbr*$_2$). The canal corresponds to the canal *"nz*$_1$*"* in *C. hoeli* (Stensiö 1927, figs. 12, 34—35; pls. 108—109; p. 233) as already assumed by Stensiö (Zych 1937, p. 84) with regard to *C. kozlowskii,* and it probably transmitted a vein from the lower side of the pectoral fin (Stensiö in Zych 1937, p. 84).

Dorsally to the opening of the canal *abr* in the pectoral area there is a fairly small opening (pl. 28:2, *nz*) in a groove in the posterior wall of the shoulder-girdle. Ventro-medially to this foramen opens a comparatively small canal *(vsc?).* In median direction from this latter opening a groove runs on to a slightly smaller opening *v.* The foramen *nz* corresponds, in *C. hoeli* and *C. exilis?* (Stensiö 1927, figs. 34—35, 52; pls. 98—99) to the opening *nz,* in *C. kozlowskii* to a lateral opening which in the figure published by Zych (1937, pl. 4:2) is conceiled in the place lettered *"a. nz",* and in *C. vogti* (fig. 17; pl. 18:1) to the opening of the canal *nz.* Following Stensiö (1927, p. 233) the canal is interpreted as having transmitted a nerve for the pectoral fin. The foramen *vsc?* is possibly the opening of the proximal division of the canal for the v. scapularis or, possibly, this canal opens in the foramen *v,* and the opening *vsc?* transmitted a vein from the inner parts of the shoulder-girdle.

Several small canals of unknown significance open into the dorso-median and dorso-postero-median parts of the pectoral area. In the most postero-ventro-lateral part of this area a small opening *vcos* is seen in *C. ibex* (pl. 28:2); it belongs probably to a canal for a superficial vein branch of the v. cornualis medialis.

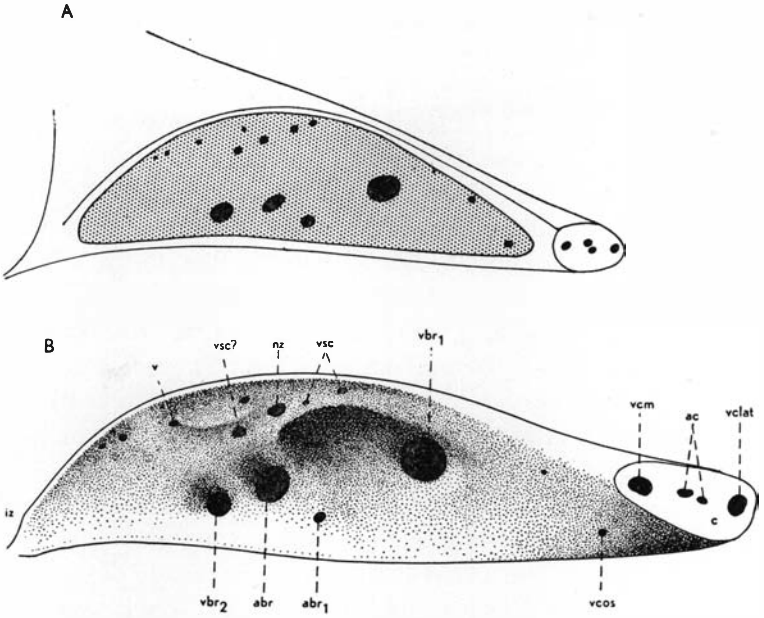

Fig. 18A, B. — Restoration of the right zonal part of the cephalic shield in *Cephalaspis ibex,* seen from behind. (A, more diagrammatic figure with the pectoral area shaded). A × 3; B × 4.

abr, opening of the main canal for the a. brachialis; *abr*$_1$, opening of a ventro-lateral branch of the canal for the a. brachialis; *ac,* canal for the a. cornualis; *c,* cornu; *iz,* inter-zonal par of the cephalic shield; *nz,* opening of a canal for a nerve to the pectoral fin; *v,* opening of a vein canal; *vbr*$_1$, opening of the canal for the main v. brachialis; *vbr*$_2$, opening of a canal for a vein from the lower side of the pectoral fin; *vclat,* canal for the v. cornualis lateralis; *vcm,* canal for the v. cornualis medialis; *vcos,* opening very probably for a superficial branch of the canal for the v. cornualis medialis; *vsc,* openings for branches of the v. scapularis; *vsc?,* opening probably of a canal for the proximal portion of the v. scapularis.

In *Axinaspis* (fig. 19; pls. 98:2-3; 99:2) the pectoral area is developed unlike that in the genus *Cephalaspis,* and this can partly be correlated with the non-development of the cornua and absence of the pectoral sinus. The general appearance of the pectoral area is described above, p. 36, and we shall here deal only with the canals opening into it.

The canal for the a. subclavia *(asubcl),* after leaving the canal for the a. efferens communis (pl. 99:2, *aeffc*), or, more exactly, the canal for the paired a. efferens communis, runs in the postbranchial wall in almost straight lateral direction and gradually turns somewhat backwards, lying above the fourth interbranchial septum (*ibr*$_5$) from behind, before it enters the ventral part of the shoulder-girdle (cf. p. 166). Here it turns rather abruptly in antero-lateral direction and travels forwards in the basal half of the zonal endoskeleton. Rather soon after

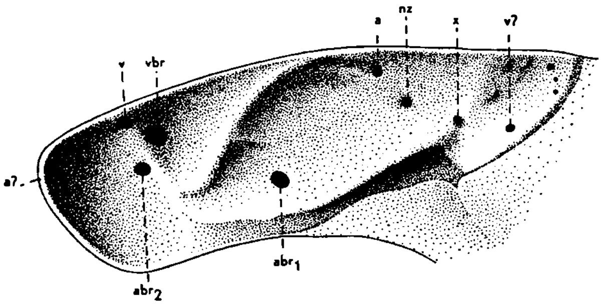

Fig. 19. — Restoration of the left pectoral area in *Axinaspis whitei.* Postero-lateral view. × 4.

a, foramen of a canal for an a. segmentalis; *a?,* foramen probably of a branch from the canal for the a. marginalis; abr_1, opening of a canal for a posterior a. brachialis; abr_2, opening of a canal for an anterior a. brachialis; *nz,* opening of a canal for a nerve for the pectoral fin; *v,* opening of a branch from the canal for the v. brachialis; *v?,* opening probably of a vein canal; *vbr,* opening of the canal for the v. brachialis; *x,* opening of a canal of unknown nature.

the bend of the canal it gives off a short and rather wide somewhat antero-laterally directed branch which opens into the pectoral area through the foramen abr_1 (pl. 98:3), and after a while it gives off an additional canal (abr_2) which opens in the anterior rather deep depression in the pectoral area. The branches of the canal *asubcl,* opening by the foramina abr_1 and abr_2, have thus transmitted arteries from the a. subclavia to the pectoral fin; they are the canals for a posterior and an anterior a. brachialis. After the exit of the canal abr_2 the main canal continues as a canal for the a. marginalis first in antero-dorso-lateral direction and then turns, opposite to the lateral angle of the shield, in anterior and slightly median direction. A small foramen *(a?)* in the most anterior part of the pectoral area very probably is the opening of a branch from this canal.

A canal from the antero-dorso-lateral part of the trunk cavity of the shield has its origin in the posterior half of the zonal endoskeleton, in the postero-lateral wall of the shield, immediately behind the posterior opening of the marginal vein sinus (pl. 98:2, *anz*); it traverses the zonal endoskeleton in lateral and slightly anterior direction, and during its course divides into two branches which open by the foramina *a* and *nz* (pl. 98:3), respectively, in the pectoral area. The foramen *a* which is situated antero-dorsally to the opening *nz* lies in the posterior end of a distinct horizontal groove which continues forwards towards the anterior oblique ridge in the pectoral area. The canal *anz* has, with regard to its dorsal position, probably transmitted a segmental artery and nerve, and the branch which opened by the foramen *a* I regard as having lodged the segmental artery which after entering the pectoral area, at least partly, continued forwards in the groove mentioned above, while the postero-ventral branch which opens by the foramen *nz* is thought to have lodged a nerve for the pectoral fin (cf. *C. kozlowskii* and *C. vogti,* figs. 16, 17).

In the anterior part of the antero-dorsal triangular depression in the pectoral area a big and short canal from the marginal vein sinus opens through the foramen *vbr* (pl. 98:3), and this canal must have transmitted a vein from the pectoral fin (v. brachialis). During its course it gives off a canal *(v)* in dorso-anterior direction which soon opens into the same depression in the pectoral area as the brachial vein canal; it lodged a vein from the dorsal side of the pectoral fin or the shoulder-girdle.

In the posterior part of the pectoral area there are several openings *(v?, x,* pl. 98:3) for small canals which have been observed mostly to traverse the zonal endoskeleton and centrally to open into the trunk cavity of the shield; the canal *v?* probably transmitted a vein and is comparable possibly to the vein canal vbr_2 in *Cephalaspis* while the nature of the other canals is obscure.

We thus find a certain resemblance in the general disposition of the canals in the shoulder-girdle of *Axinaspis* and *Cephalaspis,* and the main difference lies in the development of canals for two strong aa. brachiales in the former genus. We find furthermore that the largest canals in the pectoral area open in the anterior half of the area. On account of the configuration of the face of this area we can assume that the principal muscles of the pectoral fin were attached to it (cf. p. 36).

In *Nectaspis* very little can be said about the structure of the zonal endoskeleton; the canals for the a. subclavia and for an a. brachialis are seen (pl. 110:2, *asubcl, abr*) but it could not be ascertained if there are one or two canals for brachial arteries. From the marginal vein sinus *(vsmarg)* a small canal *(vclat?)* runs towards the lateral angle of the shield; it probably corresponds to the canal for the v. cornualis lateralis in species with cornua developed.

In *Boreaspis* some species, as e.g. *B. costata* (pls. 85; 86:2), have a long zonal part. The canal for the a. subclavia *(asubcl)* which issues directly from the aortal canal (as an a. efferens communis par, see p. 163) runs in lateral and slightly posterior direction. On reaching the zonal endoskeleton behind the marginal vein sinus *(vsmarg)* it turns abruptly in antero-lateral direction and very soon gives off a canal for the a. brachialis *(abr).* It could not be established whether there is a canal for an anterior brachial artery before it or not, but because of the extent of the zonal part it seems very likely that there really is such a canal.

It is thus beyond any doubt that also in the genus *Nectaspis* and in the *Boreaspis* species with reduced cornua and pectoral sinus, there was a (probably well developed) pectoral fin, as in the genus *Axinaspis*.

With regard to the vascular supply of the superficial parts of the endoskeletal shoulder-girdle and the pectoral fin we can in conclusion state the following: Branches from the a. subclavia supplied the pectoral fin (aa. brachiales), the lower face of the shoulder-girdle proper (r. superficialis ventralis a. subclaviae), and the cornua (aa. cornuales), while an a. segmentalis (behind the a. subclavia and the a. segmentalis occipitalis) supplied the dorsal face of the shoulder-girdle proper (aa. scapulares) and possibly, to a small degree, also the pectoral fin. Veins, emptying into the marginal vein, drained the lateral part of the cornua (v. cornualis lateralis), and veins, emptying through the v. brachialis into the widened part of the marginal vein, i. e. into the zonal part of the marginal vein sinus, drained the median parts of the cornua (v. cornualis medialis) and (secondarily) through this cornual vein parts of the dorsal face of the shoulder-girdle proper and possibly parts of the pectoral fin. Veins discharging directly into the zonal and post-zonal parts of the marginal vein sinus drained the pectoral fin (vv. brachiales) and, exceptionally *(Axinaspis),* the dorsal face of the shoulder-girdle proper, and veins to the post-zonal part of the marginal vein sinus drained the dorsal (v. scapularis) and ventral side of the shoulder-girdle proper and to a small degree also the pectoral fin.

The v. marginalis in the Cephalaspids is regarded by Stensiö (1927, pp. 185, 228, 368) as homologous with the v. superficialis longitudinalis dorsalis in *Petromyzon* and by Holmgren (1946, pp. 75—76) compared with the marginal vein in embryos of *Myxine* (cf. p. 229). The a. subclavia, a. marginalis and the brachial veins and arteries have no equivalents in recent Cyclostomes. The v. marginalis can possibly, but only functionally, be compared with the anterior superficial longitudinal vein in sharks which joins the subscapular sinus and which can be regarded as an anterior continuation of the lateral cutaneous vein (Marples 1936a, p. 321; fig. 2). The v. scapularis corresponds more or less to a dorsal branch of the dorsal pectoral cutaneous vein or to a branch opening into the anterior part of the lateral cutaneous vein in sharks (Marples 1936a, p. 324; 1936b, pp. 835, 836; figs. 3, 12). The a. marginalis can be compared with the dorso-lateral artery which from the a. subclavia runs forward dorso-medially to the gill-opening and with the dorsal superficial branchial artery from the a. epibranchialis 1, which, however, belongs to a different arterial system. In *Squalus* there is often an anastomosis between these two arteries (O'Donoghue & Abbott 1928, pp. 852, 855; figs. 5, 8). The aa. scapulares correspond functionally to the dorso-lateral artery in *Squatina* (Marples 1936b, p. 825; fig. 3) or to branches from a similar artery in *Squalus* (O'Donoghue & Abbott 1928, figs. 5, 8), but not to the scapular artery which is a deep vessel running in the dorsal wall of the coelom. The r. superficialis ventralis a. subclaviae (and other ventral superficial arteries in the shoulder-girdle) was functionally equivalent to the ventro-lateral artery, issuing from the a. subclavia in *Squalus* (O'Donoghue & Abbott 1928, fig. 8).

The pronephros component.

Traces of the pronephros component of the endoskeleton of the cephalic shield have been observed but in one case, viz. in a specimen of *Axinaspis whitei* (pl. 99:2, *prn*), and they will only be briefly mentioned here. It can be noted that the pronephros component is previously known only in *C. exilis?,* in which species it was discovered and described by Stensiö (1927, pp. 149, 244—245).

In pl. 99:2 the postbranchial wall is seen to be partly preserved as an impression of its posterior face. Between the common foramen for the oesophagus and the truncus arteriosus *(oes + tr),* and the canal for the a. efferens communis impar *(aeffc)* there is observed a small paired elevation *(prn),* corresponding to a paired depression in the posterior side of the postbranchial wall, the left half of it being slightly larger than the right one. In comparison with the corresponding parts of the postbranchial wall in *C. exilis? ("C. hoeli",* Stensiö 1927, figs. 9—10, 34—35; pls. 106—107) we find that the paired depression with regard to its position and its general shape, as far as this can be seen, corresponds to the space *"pr. nephr"* in *C. exilis?* which is called the pronephros space and interpreted as having lodged (an anterior part of) the pronephros. It can, however, be observed that although the face of the paired elevation in *Axinaspis* is not quite smooth there are no distinct grooves and ridges as those in the pronephros space in *C. exilis?.*

The sensory line system.

We have previously (p. 49) seen that the sensory line system in the Spitsbergen Cephalaspids was lodged in narrow open grooves in the exoskeleton, and that these grooves reached down into the outer division of the middle layer of the exoskeleton.

The grooves of the sensory line system found in the cephalic shields of different forms in the new material of Spitsbergen Cephalaspids agree on the whole with those described earlier in the Cephalaspids (Stensiö 1927, pp. 235—239; 1932, pp. 48—51; Heintz 1939, pp. 27—28; Westoll 1945, p. 342) but a few grooves previously known only in other Osteostraci or hitherto unknown are also discovered.

The grooves of the sensory line system observed in the Spitsbergen Cephalaspids belong to the following lines: the infraorbital line *(ifc, ifc_1)*, the supraorbital line *(soc)*, the main lateral line *(lc, lc_1)*, the dorsal lateral line *(dlc)*, the extra-lateral line *(elc)*, and three transverse lines *(stc + scc, mp, cm)*. These grooves or some of them are seen in several species of *Cephalaspis* (figs. 23, 28, 35, 51—52; pls. 5:1-2, 3; 6:1; 7:2; 10:1; 11:3, 5; 13—14; 15:2; 22:2; 28:1; 33:2; 40:1-2; 45:2; 47:2; 68:1; 114:1), in *Securiaspis* (fig 74; pls. 62:2; 64:1), *Benneviaspis* (figs. 78C—D, 80; pls. 68:2; 69:1; 70; 71:1), *Hoelaspis* (fig. 85; pl. 77:1), *Boreaspis* (fig. 86A; pls. 79:2; 81:1) and *Nectaspis* (fig. 105A; pls. 108; 110:2).

A rather characteristic trait in the Cephalaspids is the inconstant development of the grooves of the sensory lines, not only in species of the same genus but also within one and the same species. Grooves present in one specimen may be entirely lacking in another specimen of the same species. The most constantly present grooves belong to the infraorbital line, the anterior portion of the main lateral line, and the posterior transverse line. Grooves which in some cases are developed as long continuous lines are in other cases developed as a series of short or long dashes. If the short grooves become very short or dot-like, it is most often impossible to distinguish them with certainty from the openings of the mucous canal system, into which the elements of the sensory lines were sunk. This fact can possibly account for the failure to locate the sensory lines and thus also for the seeming inconstance in their appearance, which is not due to a too superficial position in the exoskeleton of the grooves in some forms (cf. Stensiö 1932, p. 48).

The groove for the infraorbital line *(ifc, ifc_1)* is composed of two divisions as in the Cephalaspids from Great Britain and Norway. The posterior of them (*ifc*, pls. 5:1-2; 7:2; 10:1; 11:3, 5; 22:2; 28:1; 33:2; 40:1-2; 45:2; 62:2; 64:1; 68:1-2; 69:1; 70:1; 71:1; 76:1; 79:2; 81:1) is running from the lateral border of the orbital opening in antero-ventro-lateral direction, ending generally at the median margin of the lateral sensory field. As the exoskeletal plates which covered the field in this place are not preserved in any specimen the distal part of the groove which generally went over these plates could not be observed. The anterior division of the groove (*ifc_1*, pls. 5:1; 6:1; 7:2; 11:5; 14; 28:1; 79:2; 81:1; 110:2) generally runs from the antero-median margin of the lateral sensory field in median direction to the median line or to a point near it; in the former case it meets its fellow of the other side so as to form a more or less continuous transverse line between the lateral sensory fields. The line in the groove *ifc_1* can be regarded as a transverse commissure between the longitudinal lines in the grooves *ifc*. In *Nectaspis* (pl. 110:2) in which the lateral sensory fields are narrow the distal part of the groove for the posterior division of the infraorbital line does not enter the (anterior) field but runs somewhat medially to it.

To judge from the disposition of the nerve canals, the neuromasts in the grooves *ifc* and ifc_1 were innervated by nerve-fibres which issued from the anterior lateralis ganglion in the trigeminus-lateralis chamber and in peripheral direction ran between the rr. maxillaris and mandibularis V (cf. pls. 6:1; 12:5; 34:1); they corresponded to the r. buccalis in the Petromyzonts. The different parts of the infraorbital line must, however, have been innervated by different nerve-branches as is evident if we compare the disposition of the grooves in pl. 11:5 and the course of the nerve canal *bu* and its antero-median branch in pl. 34:1; the nerve in the canal *bu* can only have innervated neuromasts in the groove ifc_1.

The anterior division of the infraorbital line (ifc_1) was compared by Stensiö (1932, pp. 49—50, 174) with the supposed supraorbital line in *Petromyzon* (considered homologous to the supraorbital line in fishes, cf. Stensiö 1926, p. 10). The two divisions of the infraorbital line in Cephalaspids were thus assumed to belong to two quite different sensory lines. As shown, on a different basis, by Säve-Söderbergh (1941a, pp. 534—535) and Holmgren (1942, p. 6)[1] this view is not admissible; the entire line belongs to the infraorbital line, and as in the Petromyzonts, the anterior and posterior divisions were innervated by different portions of the r. buccalis.

The anterior division of the line in the Osteostraci may, however, possibly constitute a transverse commissure, comparable to the ethmoidal commissure in fishes, as suggested by Allis (1934, p. 396) and Säve-Söderbergh (1941a, p. 535). In e.g. *Amia* this commissure is innervated by the most anterior portion of the r. buccalis (Allis 1889, p. 514; 1897, pp. 603—605; figs. 20, 30). It is therefore of interest to observe that in older Osteostraci this (supposed) commissure lay farther back on the shield than in the real Cephalaspids and was situated almost over the anterior margin of the ethmoidal region of the endocranium (e.g. *Dartmuthia, Saaremaaspis*).

In this connection we may briefly consider the anterior marginal groove found in *Trematаspis, Saaremaaspis* and *Thyestes* but as yet in no real Cephalaspid. The groove was compared by Robertson (1940b, p. 468) with the oral line in *Petromyzon* (Robertson 1940b; Holmgren 1942; circumbuccal, Razzauti 1916; Allis 1934), and by Holmgren (1942, p. 6) with the anterior part of the posterior division of the infraorbital line in *Petromyzon,* and assumed to have been innervated

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1) The anterior division of the infraorbital line, the so-called "supraorbital line" in *Petromyzon* is not innervated by lateralis fibres in the n. profundus (Johnston 1905a, pp. 156, 186) but by an anterior portion of the r. buccalis (Allis 1924, p. 263, 1931b; 1934, p. 362; Holmgren 1942, p. 6; Lindström 1949, p. 388).

by the r. buccalis. In view of the disposition and the branching of the nerve canal *bu* in *C. exilis* (pl. 34:1) it seems most probable that the anterior marginal groove really lodged neuromasts innervated by an anterior branch of the r. buccalis. The homologization of the line with a definite line in *Petromyzon* is difficult as it is very probable that also an anterior part of the oral line is innervated by a branch of the r. buccalis (cf. Allis 1934, p. 363; fig. 1; Lindström 1949, p. 382); it seems, however, most plausible to follow Holmgren (1942) and regard it as a branch of the infraorbital line. The lateral branch from the infraorbital line in *Didymaspis* (Stensiö 1932, fig. 61A), found by me also in a specimen of *Thyestes verrucosus* (p. 552), probably represents a connecting link between the infraorbital line and the anterior marginal line (cf. Holmgren 1942, p. 6). Possibly the main lateral line, the posterior division of the infraorbital line, and the anterior marginal line form parts of a single longitudinal unit, to which the anterior division of the infraorbital line is the most anterior transverse commissure.

The grooves of the main lateral line (*lc*, lc_1, pls. 5:1; 7:2; 10:1; 11:3, 5; 22:2; 28:1; 33:2; 45:1; 62:1; 64:1; 68:1-2; 69:1; 70; 71:1; 76:1; 77:1; 79:2; 108; 110:2; 114:1) start from the postero-lateral corner of the orbital opening or from its vicinity. The line runs first in postero-ventro-lateral and then turns in a straight posterior direction. It usually ends at a posterior transverse series of grooves *(stc, scc)* but in *Benneviaspis* (pls. 69:1; 70:2; as noted by Stensiö 1927, p. 236), in *Securiaspis* (pl. 64:1) and in *Boreaspis* (pl. 79:2) it is also found running on the inter-zonal part of the shield near the postero-lateral angle.

The anterior, more or less transversally running, division of the line (lc_1, pls. 10:1; 69:1; 70:1; 76:1; 79:2; etc.) was considered by Stensiö (1927, pp. 236—237) to be a transversal groove corresponding to the jugal or preopercular canal in fishes (cf. Stensiö 1947, p. 20; Holmgren & Pehrson 1949), by Robertson (1938a, p. 195) called the postorbital line, intercalated between the infraorbital and the main lateral line (cf. Goodrich 1930, p. 740, and Zych 1937, p. 89), and by Holmgren (1942, p. 7) regarded as a portion of the main lateral line (cf. Säve-Söderbergh 1941a, p. 534). It seems most natural to regard it as an anterior continuation of the main lateral line and, as it doubtless, at least partly, was innervated by a posterior branch of the r. buccalis, running in a canal, corresponding to the canal "$n.\ bucc._3$" in *C. kozlowskii* (Zych 1937, pp. 87, 88—89; pl. 2) it corresponds to the otical portion of the main lateral line in fishes.

A part of this anterior division reaches in some cases *(Benneviaspis*, pl. 69:1, *cm;* cf. Stensiö 1927, fig. 76A; 1932, fig. 55; cf. also *Nectaspis,* pl. 108, *cm,* and *C. aarhusi,* fig. 23) farther laterally than to the anterior end of the posterior division *(lc),* and this lateral continuation can possibly be regarded as a transverse line joining the main lateral line. As it seems very improbable that this line was innervated by any fibres from the anterior lateralis ganglion (r. buccalis) but rather by lateralis fibres associated with the n. glossopharyngeus, it probably did not correspond to the preopercular line or any other sensory line on the cheek in fishes (cf. Stensiö 1947; Holmgren & Pehrson 1949). It can possibly be compared with a series of two rudimentary neuromasts connecting the infraorbital line with the suprabranchial line, found by Holmgren (1942, p. 4) in a specimen of *Petromyzon fluviatilis;* the innervation of these organs is, however, by Holmgren assumed to be hyomandibular.

The posterior portion of the main lateral line (in the groove *lc*) was doubtlessly innervated in *Cephalaspis* by lateralis fibres belonging to the posterior lateralis nerve and accompanying the n. glossopharyngeus. The innervation of the most posterior cephalic portion of the line (in the postero-lateral corner of the inter-zonal part of the shield in *Securiaspis, Benneviaspis* and *Boreaspis)* was probably effectuated by a lateralis branch in the n. vagus (cf. the course of the groove *XII in C. doryphorus,* pl. 39:1, 3).

In *Tremataspis* Robertson (1938a, p. 197) found a sensory line running backwards from a point just behind the posterior lateral sensory field; it was called the extra-lateral line. A longitudinal groove *(elc)* which is thought to constitute an anterior portion of this line is found in a few *Cephalaspis* species (figs. 23, 28, 51; pls. 7:2; 28:1). In *C. signata* in which it is best developed, the groove *elc* runs from the lateral part of the transverse groove *scc* in anterior direction to a point near the median margin of the lateral sensory field (pl. 28:1); in *C. broughi* there is only a short longitudinal groove situated behind the groove *scc* in front of the pectoral sinus (pl. 7:2) and in *C. aarhusi* an obliquely disposed groove possibly represents the same line (or is a forwardly curved portion of the scapular line). It can here be noted that the extra-lateral line is found also in *Thyestes;* here it consists of two grooves between the posterior end of the lateral sensory field and the antero-median corner of the pectoral sinus (fig. 107). To judge from the disposition of the extra-lateral line in *Tremataspis* and *Thyestes,* the suggestion by Holmgren (1942, p. 8) that the line posteriorly turned over to the ventral side of the shield and continued in the ventral lateral line seems rather probable.

The extra-lateral line in *Tremataspis* was regarded by Holmgren (1942, p. 35) as a remainder of the suprabranchial line in *Petromyzon* (cf. Merkel 1880, pl. 2:1; Alcock 1898, fig. 1B; Johnston 1905a, pl. 5; Razzauti 1916, fig. 1, serie interbranchiale; Stensiö 1926, fig. 7B, *ibr;* Holmgren 1942, fig. 1), and in view of the conditions in the

Cephalaspis species just mentioned the homologization of the extralateral line in the Osteostraci and the suprabranchial line in *Petromyzon* seems to be a most plausible interpretation.

In *C. doryphorus* a dorsal longitudinal line is developed; it consists of two grooves, an anterior short groove running in posterior direction from the postero-lateral corner of the dorsal sensory field, and a posterior somewhat longer, sigmoidally bent groove (pl. 40:1, *dlc*). This line must have been innervated by a r. lateralis vagi (cf. p. 116), and it certainly corresponded to the dorsal lateral line in *Petromyzon.* It belongs to the same longitudinal line as the dorsal lateral line in *Tremataspis* (Patten 1903, fig. 9; Stensiö 1927, p. 307; fig. 83B; Robertson 1938a, p. 197; fig. 1). It is not found in any other Cephalaspid.

In *Tremataspis* a pair of short, obliquely set, grooves (the "suprapineal groove") occurs antero-laterally to the dorsal sensory field (Patten 1903, p. 21; fig. 9; Stensiö 1927, p. 307; fig. 83B, *pc;* Robertson 1938a, p. 195; fig. 1, *s. p. c.*) and an exactly corresponding pair of grooves is found in *Hoelaspis* (Stensiö 1927, fig. 77, *pc;* cf. fig. 85, this paper). In a specimen of *Benneviaspis* a similar groove is also described by Stensiö (1927, p. 238; fig. 76) but it seems very doubtful if it really corresponds to the groove in *Tremataspis* and *Hoelaspis,* just mentioned (cf. below). This line is not found in other Osteotraci. It was assumed by Stensiö (1927, p. 238) to have been innervated from the n. lateralis anterior and thought most probably to have corresponded to the pineal (suprapineal) line in *Petromyzon.* As, however, this line in *Petromyzon* is now shown to be innervated by lateralis fibres accompanying the n. glossopharyngeus (Lindström 1949, p. 401) and since the assumption of such an innervation of the line in the Osteostraci seems out of question (cf. p. 79), the line cannot be equivalent to the pineal line in *Petromyzon.* It may represent a posterior portion of the supraorbital line or the anterior pit-line in fishes (these alternatives are also mentioned by Stensiö 1927, p. 238). In fishes the anterior pit-line develops as a posterior division of the supraorbital line and is, like this, innervated by the r. ophthalmicus lateralis (Allis 1889; cf. Devillers 1944; Lekander 1949, pp. 8—18, 22—23; Pehrson 1949). The line in the Osteostraci can, however, possibly represent the rest of a cross-commissure which once connected the supraorbital and the infraorbital (or the main lateral) lines.

A groove *(soc)* belonging to the supraorbital sensory line is found only in a specimen of *C. excellens* (pls. 13; 15:2). It runs from the pineal fissure in anterior direction with a slight lateral bend towards the antero-lateral side of the opening for the hypophyseal duct; the groove thus lies on the ethmoidal part of the head. The line was certainly innervated by fibres corresponding to the r. ophthalmicus (superficialis) lateralis. No certain supraorbital line is present in the Cyclostomes (cf. Holmgren 1942, p. 4; Lindström 1949, p. 335).

Of the transverse sensory lines we have mentioned above that the anterior portion of the infraorbital line possibly represents an anterior commissure and have also commented upon the groove *cm* found in a few specimes.

In *Benneviaspis holtedahli* Stensiö (1927, fig. 76A) has figured three pairs of transverse grooves meeting the dorsal sensory field. The anterior one of them *("pc")* was homologized with the groove *pc* in *Tremataspis* and *Hoelaspis,* but it is to be noted that the groove in question has another disposition than the groove *pc* in these forms. and that in *B. lankesteri* (Stensiö 1932, pl. 49:1; cf. fig. 55 in which the line lies too far posteriorly) a groove which quite certainly corresponds to it is labelled *"cmm"*, and thus considered to correspond to the groove, lettered *mp* in this paper in other Cephalaspids *("cmm"* by Stensiö; in *Tremataspis* called the anterior transverse line by Robertson 1938a).

The groove *mp* of the anterior transverse sensory line (pls. 11:3, 5; 28:1; 40:1; 68:2; 79:2; 110:2) which generally is very short abuts against the lateral margin of the dorsal sensory field in its anterior half. The neuromasts in this line were probably innervated by a lateralis branch which accompanied the branchial ramus of the n. glossopharyngeus (cf. p. 206), and this line corresponded to the middle head line of pit organs in fishes, as supposed by Stensiö (1927, p. 238; cf. 1932, p. 51) and to the pineal line in *Petromyzon.*

The groove *cmm* in the specimen of *Benneviaspis holtedahli* (Stensiö 1927, fig. 76A), mentioned above, has no equivalent in any other form in the Osteostraci; if it is not a freak, the line may possibly correspond to the posterior pit-line on the head in fishes.

The posterior transverse groove or series of grooves *(stc, scc,* pls. 7:1; 10:1; 11:3, 5; 22:2; 28:1; 33:2; 40:1; 45:2; 47:2; 62:2; 68:2; 69:1; 70; 71:1; 79:2; 108; 110:2) runs from the posterior part of the dorsal sensory field near the opening for the ductus endolymphaticus (in some Cephalaspids from Great Britain it was found to start on the plates of the dorsal sensory field, Stensiö 1932, p. 51) in lateral or ventrolateral direction ending at or near the median margin of the lateral sensory field; here it meets the longitudinal extra-lateral line when this line is present. The line generally consists of several (often three) grooves but in *Benneviaspis* it sometimes forms a continuous groove (pls. 68:2; 71:1). We can distinguish between a median portion of the line, lying medially to the main lateral line, and a lateral one. lying between the main lateral line and the lateral sensory field.

The median portion *(stc)* of the posterior transverse line is most probably equivalent to the posterior transverse series of neuromasts in the head of *Petromyzon* (Merkel 1880, p. 12:2; Razzauti 1916, fig. 2, seconda serie occipitale; Stensiö 1926, fig. 7A; Holmgren 1942, fig. 1, supratemporal commissure), corresponding to the supratemporal commissure or the posterior pit-line on the head in fishes (Stensiö 1927, p. 237; 1932, p. 51) and is therefore called the supratemporal line. The lateral portion *(scc)* of the line forms a lateral extension of the supratemporal line over the shoulder-girdle. It was called by Holmgren (1942, pp. 6, 26, 42) the scapular line, and was compared with a similar line in some Teleosts. To judge from the conditions in *C. doryphorus* and *C. excellens* with regard to the nerve canals and grooves *IXl* and *Xl* and their branches, the supratemporal line was innervated by lateralis fibres which accompanied the n. vagus, while the scapular line was supplied by lateralis fibres issuing together with the n. glossopharyngeus.

The sensory lines in the Osteostraci can be interpreted fairly well in the light of our knowledge of the sensory lines in recent Petromyzonts (the neuromasts in *Eptatretus* have not a disposition which does allow a comparison with those in other vertebrates, cf. Ayers & Worthington 1907), and they thus seem in both groups to have been disposed after the same general plan.

In the disposition of the sensory lines on the dorsal side of the cephalic shield in the Osteostraci we can make out a generalized pattern, or arrange the lines so as to fit such a pattern, consisting of main longitudinal lines, connected by cross-commissures (cf. Allis 1934, p. 410; Säve-Söderbergh 1941a, p. 530; Holmgren 1942, pp. 29—30).

We can thus discern three main longitudinal stems and four (or five) cross-commissures. The inner, median, longitudinal stem consists, according to this view, of the dorsal lateral line and the supraorbital line. The middle longitudinal stem is made up of the main lateral line, the posterior division of the infraorbital line and the anterior marginal line. The outer, lateral, longitudinal stem is represented by the extra-lateral line. The cross-commissures which generally are short and not complete would consist of the following lines, viz. *a,* the anterior division of the infraorbital line, *b,* the lines *mp* and (possibly) *cm, c,* the supratemporal and scapular lines, *d,* the so-called transverse commissure (between the dorsal lateral lines in *Tremataspis),* and furthermore possibly the «suprapineal line».

Regarded in this way the disposition of the sensory lines in the Osteostraci can be brought in accordance with that of the Heterostraci (which, however, is not uniform in the different forms). With the discovery of the sensory line system in *Traquairaspis ("Phialaspis",* White 1946a) was found a type which together with other Heterostraci permits a comparison to be made on general lines between the sensory line systems in the Osteostraci and the Heterostraci. The branchial line in *Traquairaspis* thus corresponds to the extra-lateral line in the

Osteostraci (cf. Holmgren & Pehrson 1949, p. 307). The lateral dorsal (the main lateral line) and the infraorbital lines, found best developed in *Pteraspis* (the lines, lettered *ll* and *ifsv* in fig. 5A and *lc, ot, ifsv, ifsh* in fig. 9, Säve-Söderbergh 1941a), are represented in the Osteostraci by the middle longitudinal stem. In the Heterostraci the median dorsal line (the median longitudinal line on the dorsal plate of which the so-called dorsal lateral line, Holmgren 1942, figs. 8—9, forms a part) together with the supraorbital line and part of the pineal line (the lines lettered *dl, pp,* ap_2, *apc, soc* in fig. 5A, Säve-Söderbergh 1941a) corresponds to the inner longitudinal stem in the Osteostraci. The supposed anterior cross-commissure (the anterior division of the infraorbital line) has no equivalent in the Heterostraci; the "suprapineal line" is possibly represented by the line lettered *x* in figs. 5, 9 in Säve-Söderbergh 1941a (the line between *br* and *Pb* in fig. 3, Kiær & Heintz 1935; *co* in fig. 41, Zych 1931), and to this cross-commissure belongs also the median part of the pineal canal (cf. Zych 1931, figs. 41, 49); the lines *mp* and *cm* correspond to the line *mp* in *Poraspis* (Säve-Söderbergh 1941a, fig. 5A; tc_2, Kiær & Heintz 1935, fig. 3) and the cross-commissure formed by the supratemporal and scapular lines is probably equivalent ot the next transverse line in the Poraspids (*s. com?*, tc_3).

The correlation of the sensory lines in the two principal fossil groups of the agnathous vertebrates, given above, is of course only tentative as comparisons can only be made along much generalized and simplified lines, and as we know rather little of the innervation of the different lines in the Osteostraci and hardly anything at all in the other group (cf. p. 563).

The sensory fields.

The sensory fields ("electric fields", Stensiö) are, as well known depressed areas on the dorsal side of the cephalic shield in the Osteostraci, covered by independent exoskeletal bone plates, and constitute one of the most distinguishing features in the organization of this group. Correlated with the presence of the fields is the development of canals for strongly developed nerves.

The general shape of the fields and their disposition on the shield have been dealt with by Stensiö (1927; 1932) and in the present paper in the chapter on the external features of the shield. The minute structure of the fields has been treated in the chapter on the exoskeleton (cf. also Stensiö 1932, p. 47; Denison 1947, p. 356), and these descriptions will not be repeated here. It will only be noted that the variation in the number of the lateral sensory fields is much greater in the group than was assumed earlier, and we have thus within the family forms with one, two, three or four pairs of lateral fields. This variation contrasts with a great constancy in the disposition of the nerve canals for the fields in question.

This chapter will be devoted to a discussion of the nature of these fields, and the various opinions, put forward in an attempt at an interpretation in this matter.

The fields were considered by Stensiö (1927, p. 243) to have been electric organs, because of a certain superficial resemblance to the electric organs in *Torpedo* (the most obvious resemblance lies, however, in the shape and disposition of the nerve canals for the lateral sensory fields in the Cephalaspids and the electric nerves in *Torpedo,* cf. Robertson 1938a, p. 200; Bohlin 1941, p. 543; Westoll 1945, p. 344; Denison 1947, p. 357), and because he was unable to imagine their special function if they were sensory organs. Among later authors who have discussed the matter the opinions are much at variance or most often undecided, and the fields are often designated by non-committal terms, as "dorsal and lateral fields" (Robertson 1938a) or "cephalic fields" (Bohlin 1941). When Stensiö (1927, p. 243) refers to the resemblance of the "electric fields" in the Cephalaspids to the electric organs in *Torpedo,* he, however, also points out that the supposed electric organs in the Cephalaspids could not, like those in most fishes, have arisen from (striated) muscles but must have been formed from the basal part of the corium or from a tissue beneath it or from both; they would thus be comparable to the electric organ in *Malopterurus* which is situated in the corium (the source of the electric organ in this fish is, however, as yet unknown, cf. Bohlin 1941, pp. 546—547; Stuart & Kamp 1934a; Rauther 1937a, pp. 637—638; Kappers 1947, p. 172).

Bohlin (1941) remarks that the "volume of the electric organs, if they were such, in the Cephalaspids was very small", and Westoll (1945, p. 344; cf. Parker & Haswell 1940, p. 127) finds it impossible to understand the existence of a muscle-mass (from which the electroplaxes evidently were thought to have arisen) in the "electric" fields; in fact, the organ must have been very thin. In *Tegaspis kolleri* (in which the cephalic shield attains a length of about 14 cm) the height of the cavities between the exoskeletal plates and the endoskeleton in the lateral sensory field is at most 0.48 mm, and the distance between the basal partitions in the plates and the endoskeleton is 0.23 mm; in *Tremataspis mammillata* in which species the cephalic shield is 35—40 mm in length (Robertson 1938a, p. 289) I have measured the height of the basal cavities to be 0.06 mm.

We find now that the electric organ in *Malopterurus* occupies a very large place in the corium, and that in other fishes the electric organs (probably always developed from rudiments of somatic or visceral musculature) generally are very voluminous; in *Raja radiata,* however, the electric organ is very small but comparatively deep (Ewart 1888). The small size of the organ in the Cephalaspids cannot directly be taken as a proof against the hypothesis of their nature as electric organs, but if we consider the very insignificant height of the basal cavities in which the electroplaxes should have been situated (and the incomplete subdivision of the space between the exoskeletal plates and the endoskeleton would remind somewhat of the compartments in the electric organ in *Raja,* cf. Ewart 1892) it seems wholly improbable that the fields in the Cephalaspids could have lodged even a very slightly developed electric organ. To this must be added that, as noted by Bohlin (1941, p. 546) "there must have been a very remarkable disproportion between the quantity of electric tissue and the nerves connected with it". The nerves for the fields in the Osteostraci were, as previously emphasized, hypertrophied, compared with the other cranial nerves.

In recent fishes as in the Torpedinids, *Malopterurus,* and *Astroscopus* (Fritsch 1887, pp. 21—28, cf. Stendell 1915; Fritsch 1890, pp. 93—94, cf. Stuart & Kamp 1934a; Ballowitz 1899; Dahlgren & Silvester 1906; Stuart & Kamp 1934b; Haller 1934, fig. 534; Kappers 1947, p. 149; figs. 86—87) we find that hypertrophied electric nerves are correlated with an excessive development of the electric organ. In *Torpedo* the motor nucleus of the electric nerves attains an enormous volume (cf. Kappers 1947, pl. 117); in the Cephalaspids we cannot find any indications as to an excessive development of the motor nuclei (cf. Franz 1929, p. 63). In *Electrophorus ("Gymnotus")* which also has an enlarged electric organ, as well as in the Rajids and the Mormyrids, the organs are supplied by numerous often strongly developed nerves (Fritsch 1891, pp. 947—952; Ewart 1892b, cf. Belobodorova 1928 and Bodrova 1939; Dahlgren 1914, pp. 181—185; Kamp & Stuart 1934, p. 252).

The electric organs in fishes are innervated by (somatic or visceral) motor fibres (with regard to *Malopterurus,* cf. Kappers 1947, p. 172), and if the fields in the Osteostraci really were electric organs they must have been innervated by motor nerves. Now we have previously seen that the nerves for the lateral fields must have been provided with a basal ganglionic mass in the proximal part of their canals or in the vestibulum, and it was thus demonstrated that the nerves were sensory in function. This furnishes, I think, independently of other indications, definite proof for the view that the lateral (and consequently also the dorsal) fields cannot have been electric organs but must have been special sensory organs.

The organs which were present in the sensory fields of the Osteostraci have no direct equivalent in recent vertebrates, and all comparisons with cutaneous sensory organs in these forms must have reference only to the most general traits in their structure; more detailed comparisons as e. g. with nerve-sacs or ampullae (Wiman 1918; Jaekel 1929; Bohlin 1941) appear too strained.

Concerning the theories put forward favouring a sensory nature of these fields in the Osteostraci, we can note that Wiman (1918) compares the organs with the nerve-sacs in the Acipenserids (cf. Merkel 1880, pp. 36—39; Luther 1913, pp. 14—17; Disler 1939), Bohlin (1941) associates them with the ampullae of Lorenzini, found principally in the Elasmobranchs (Merkel 1880, pp. 39—48; Ewart 1892a, fig. 2; Daniel 1922, pp. 273, 292—294; Allis 1923, pp. 201—203; Lekander 1949, pp. 60—62; etc.; cf. also Sand 1938, pp. 524—528), and Westoll (1945) suggests that they were receptors of vibratory stimuli, thus with the same function as the sensory line (and the acusticus) system. Common to these theories is that the organs (irrespective of what their function might have been) are assumed to belong to the (acustico-) lateralis system (cf. also Jaekel 1929, p. 110). This is evidently also the view of Haller (1934, p. 661) who regards the nerves for the sensory fields as derivatives of the n. lateralis anterior.

The sense organs in the skin (and the mucosae) belong, according to Johnston (1902b; 1905b, pp. 194—197; cf. Herrick 1903a, pp. 121—124) to two different categories, viz. the neuromast organs of the somatic sensory (lateralis) system and the organs (taste-buds, end-buds) of the visceral sensory system.

We find now that the organs of the lateralis system in fishes can develop into a multiplicity of diverse structures (sensory line organs, pit-organs, ampullae, vesicles of Savi, nerve-sacs, glandiform organs, mormyromasts, etc.); in some cases they are, as mentioned by Bohlin (1941) with regard to the ampullae of Lorenzini, aggregating in definite groups or fields. The function of these different organs is by no means elucidated (the sensory lines are greatly stimulated by vibrations of low frequency but respond also to touch and pressure, Sand 1937, and also to thermal changes, Rubin 1935; the ampullae of Lorenzini are temperature receptors, Sand 1938). In some fishes, the Mormyrids, the lateralis nerves which supply special lateralis organs (mormyromasts, bulbous organs, Cordier 1938; Gérard 1940) are hypertrophied (Stendell 1914; Franz 1920, p. 6; Sprenkel 1915, pp. 33—39), and with this hypertrophism of the nerves is correlated an excessive development of the static centres in the valvula cerebelli (Franz 1912; Sprenkel 1915, pp. 29—30, 38, 41—42; Suzuki 1932; Kappers 1947, p. 153); cf. also *Megalops* (Horst 1926) and the Macrurids (Pfüller 1914).

Before making any comparisons with the Cephalaspids, we shall consider the other system of sensory organs and their central connections, the special visceral system with its receptor organs, the taste buds, sometimes developed as cutaneous taste-buds (end-buds; distant receptors of chemical stimuli); this system can also in some fishes achieve an extreme development (Kingsbury 1897; Herrick 1903a; 1903b; 1905; 1908, pp. 163—164; 1944, pp. 320—326; Goodrich 1930, pp. 730—732; Kappers 1914; 1947, pp. 164—166). In some Teleosts (Cyprinids) with strongly developed gustatory organ in the roof of the mouth the visceral sensory centres of the glossopharyngeal and the vagus nerves in the medulla oblongata are excessively developed (cf. Herrick 1905, fig. 3; Haller 1934, figs. 32—35). In others (Silurids) with cutaneous taste-buds (often distributed over the whole body) these organs are all innervated by the n. facialis (cf. besides the authors cited above, Sprenkel 1915, pp. 12—15; Haller 1934, pp. 667—670), "so that its gustatory root is the largest nerve of the body" (Herrick 1944, p. 323).

The nature of the cutaneous end buds, irregularly distributed, particularly on the head, in adult Petromyzonts (Merkel 1880, pp. 65—67; Johnston 1902a, p. 46; 1905a, p. 188; Razzauti 1916, pp. 35—40) is uncertain, and there are strong indications that they are not homologous to the taste-buds in fishes (Lindström 1949, pp. 424—425).

If we now return to the sensory fields in the Osteostraci, we find that the elements of the sense organs in question were restricted as to their distribution to sharply defined areas, and that they must have been situated in (or just beneath) the corium, thus sunken rather far below the surface, furthermore that they were supplied by strongly developed (hypertrophied) nerves, which at least peripherally lay very superficially and very probably constituted a specialized part of the n. facialis (or acustico-facialis; cf. Stensiö 1927, p. 197).

The taste-buds in fishes have always a superficial position in the epidermis, they are never confined to definite areas or fields when developed as cutaneous sense organs, they are innervated by visceral sensory fibres which generally are situated medially in the nerve, and when the nerves are strongly developed they cause hypertrophism of their centres in the medulla. All these facts speak against the view that the sensory fields in the Osteostraci belonged to the same system; there is nothing in the shape of the cavum cerebrale in the Cephalaspids indicating an excessive development of any part of the medulla oblongata. The only resemblance is the innervation by thick branches of the n. facialis (in fishes this regards the innervation of the cutaneous taste-buds). It can be noted that in the Cyclostomes the visceral afferent column in the medulla has no differentiated gustatory centre which is considered a primitive trait (Jansen 1930; Barnard 1936; Herrick 1944; cf. Lindström 1949, p. 425).

On the other hand we find that the organs belonging to the lateralis system are often sunk deeply beneath the skin, sometimes wholly separated from the epidermis (vesicles of Savi); the ampullae and the nerve-sacs form in some cases well defined groups (the groups of ampullae in *Chlamydoselachus* are by Bohlin 1941 compared with the sensory fields in the Osteostraci). Exaggerated development of the lateralis nerves is also met with in fishes, correlated with hypertrophism of their cerebellar centres. In the Cephalaspids, Stensiö (1927, pp. 138, 140, 144) has shown that the cerebellum must have been very well developed, a fact which strongly contrasts with the conditions in recent Cyclostomes in which the cerebellum is very small or virtually absent (cf. Johnston 1902a; Stefanelli 1939; Larsell 1947; Heier 1948). If we remember the general view that the cerebellum primitively constituted a continuation and further development of the area statica in the medulla (cf. Horst 1926, p. 44; Larsell 1929, pp. 297—299, 324; Kappers 1934, p. 287), and consider the conditions in the Mormyrids with regard to the correlation between the development of the cerebellum and the nn. laterales, it is tempting to assume that the strong development of the cerebellum in the Cephalaspids was correlated with the development of the sensory fields and their hypertrophied nerves, and that these latter belonged to the lateralis system, the sensory fields having been the seat of a special kind of sensory organ within this system.

We thus find that there are several indications for considering the sensory fields as specialized neuromast organs (of unknown function) and their nerves as a differentiated part of the n. lateralis (anterior; cf. Haller 1934, p. 661). Against this view can, however, be objected that the anterior lateralis ganglion was well developed and lay wholly separated from the facialis ganglion, and that it could not have taken any part in the innervation of the sensory fields. On the other side, this ganglion represents only the ganglion for the r. ophthalmicus superficialis lateralis and the r. buccalis or the combined dorsal (anterior) lateralis ganglion for these nerves in fishes (cf. Herrick 1899, pp. 288, 429; Cole 1896, pl. 1, see also Haller 1934, fig. 543; Landacre 1916, pp. 30—35; Norris & Hughes 1920, pp. 339—346; etc.; cf. also Johnston 1905a, p. 163 with regard to *Petromyzon)* while no traces of the ventral (posterior) preauditory lateralis ganglion or its nerves have as yet been detected in the Cephalaspids. It is to be observed that the various excessive developments of the lateralis system in recent fishes apparently only affect the normal sensory lines and their central connections but that in the Osteostraci the sensory fields constituted a special system coexistent with the normal sensory line system.

Another point to be considered in this connection is that the ganglia of the nerves for the sensory fields (as we have seen previously, p. 84) occupied a ventral place in the vestibulum, and that the n. facialis lay dorsally and superficially to these nerves (cf. Stensiö 1927, figs. 18—19, 23—25, 27). If the latter really constituted a transformed portion of the lateralis element of the facial nerve, they should presumably have taken a more superficial position and have lain superficially and laterally to the main nerve (Haller 1934, pp. 659, 661; cf. however, Landacre 1914, p. 604). The exact position of the facialis ganglion is, however, unknown, and the (main part of the) n. facialis soon took a more ventral position and went down to the oralo-branchial chamber; in their peripheral course the nerves for the lateral sensory fields lay very superficially.

In conclusion we can say with regard to the dorsal and lateral fields in the Osteostraci that they were not electric organs but lodged special sensory organs, possibly (or probably) belonging to the lateralis system (their function is however wholly unknown and will so remain).

The cranial nerves.

This chapter will contain a summary of what can be deduced from the canals, interpreted as nerve canals, as to the structure and disposition of the cranial nerves in the Cephalaspids. It is based upon the researches of Stensiö (1927) and supplemented with the complementary examinations communicated in the present paper, which in several cases have led to deductions different from those of Stensiö.

An attempted restoration of the brain and the cranial nerves in a *Cephalaspis* species is given in fig. 20 (cf. Stensiö 1927, fig. 43).

The n. olfactorius (I) had no canal of its own; it certainly was very short, since the olfactory organ lay immediately in front of the bulbus olfactorius, but whether it was developed as in the Petromyzonts or as in the Myxinids (with one or several roots) is unknown.

The n. opticus (II) pierced the connective tissue, separating the orbit from the cavum cerebrale in about the middle of the fenestra optica. It probably had an antero-lateral course from its exit in the hypothalamus.

The n. oculomotorius (III) left the side of the cavum cerebrale in a short canal slightly before the dorsum sellae and went directly to the postero-median part of the orbit; the exit of the canal from the cavum cerebrale is seen in pl. 57.

The n. trochlearis (IV) had a fairly long intracranial passage before it pierced the lateral wall of the cavum cerebrale rather high up; it crossed the v. cerebralis anterior just as it passed from this cavity or somewhat medially to this point. The canal for the nerve opens into the postero-dorso-median part of the orbit (it did not, as in recent Petromyzonts, enter the orbit together with the n. trigeminus). The exit of the canal from the cavum cerebrale is seen in pl. 57 and its opening into the orbit in pl. 31:1.

The n. trigeminus (V) was probably, as in recent Cyclostomes, composed of a n. profundus (r. ophthalmicus, V_1) and a n. trigeminus proper (r. maxillo-mandibularis, V_2, V_3).

Nothing definitely can, however, be said about the n. profundus. It very probably was only slightly developed, and no canals which can be assigned with certainty to this nerve are found. Some canals in various species have tentatively been regarded as such canals (pls. 10:1; 37; 38:2; 106—107); if they really transmitted branches of the n. profundus, the nerve must have innervated the antero-dorsal superficial parts of the shield, in the region situated between the orbits and the antero-median ends of the lateral sensory fields. The ganglion for the n. profundus probably was situated in the (antero-)dorso-median part of the trigeminus-lateralis chamber; the root fibres pierced the cranial wall, running in a canal of their own (*Vsa,* pls. 31:1; 57), or in company with the sensory root of the n. trigeminus proper in the canal *Vs* (fig. 10; pls. 15:1; 17) or with all the roots of the trigiminus-lateralis complex in the canal *rV* (fig. 12; pl. 112:1). As to its composition the nerve must have been entirely somatic sensory and on the whole much in agreement with the corresponding nerve in recent Cyclostomes. Its area of distribution seems, however, to have been more restricted than in these forms. On principle it differed very probably in no way from the corresponding nerve or ramus in other vertebrates; in the Osteostraci it certainly was not a branchial nerve (cf. Stensiö 1927, pp. 108—109, 156, 199, 202—203, 354). It is to be noticed that the n. profundus (r. ophthalmicus) in *Petromyzon* never behaves as a branchial nerve; in the ontogenetic development all rudiments of a visceral branch and an epibranchial placode are lacking (Koltzoff 1902, pp. 487, 518).

The n. trigeminus proper (V_2, V_3, r. maxillo-mandibularis) was strongly developed. It consisted of two independently developed rami, an anterior mixed sensory and motor ramus, here called the r. maxillaris (V_2), and a posterior, exclusively motor ramus, called the r. mandibularis (V_3).

The ganglion of the r. maxillaris (g. gasseri) was situated in the trigeminus-lateralis chamber in which it very probably occupied a central position between the profundus ganglion on its median and the anterior lateralis ganglion on its lateral side. The sensory root fibres left the cavum cerebrale in the canal *Vs* (fig. 10; pls. 15:1; 17; 31:1; 57) either together with the n. profundus root or in a separate canal. A portion of the motor trigeminus, forming part of the r. maxillaris, also went through the trigeminus-lateralis chamber. It entered this chamber after having passed through the canal *Vm* (fig. 10; pls. 8:2; 14; 15:1; 16—17; 31:1; 39:1; 40:3; 57) or issued from the cavum cerebrale by one or possibly several canals *(Vma)* which join the canal *Vm* (fig. 10; pl. 57:2-3. The mixed nerve, r. maxillaris, which emerged from the trigeminus-lateralis chamber, went through the orbit, lying closely to the floor of it, in which it in some cases caused an impression in form of a groove (pls. 3:2; 4:1; 8:2; 14; 15:1, 3-4; 16:1; 17; 39:1; 40:3; 81:1; 83:1; 86:2). The nerve left the orbit in piercing its anterior or antero-lateral wall and traversed the ethmoidal region of the endocranium in a canal of its own, entering the rostral part of the visceral endoskeleton (pls. 3:2; 4:1; 6:2; 8:2; 9:7; 10:2; 11:4; 14; 15:3-4; 19:2; 23:2; 25:2; 30:1; 36—37; 38:2; 61; 62:1; 63:2; 64:2; 66; 67:1; 68:3; 69:1; 70; 71:2; 77:2; 78:1; 82:2; 83:1; 84:2; 85; 86:2; 89:2; 90:3, 5; 93:2; 94—95; 97:3; 98:1; 100:1; 102:1; 103:4; 106—107, 110). During its passage it gave off several superficial branches with general cutaneous fibres. Some of the general cutaneous nerve fibres from the ganglion gasseri went out into the visceral endoskeleton independently of the main nerve trunk, either in narrow canals of their own (cf. the anterior ones of the canals lettered *n* in pls. 14; 16:2; 36:1; 37; 59:1; 60) or in the canals for the first nerve for the lateral sensory field and for the r. mandibularis. The nerve entered the oralo-branchial chamber as a main trunk or after having split into two or several branches and thus through one or several openings in the roof of this chamber (pls. 10:2; 13; 17; 82:1; 83; 87:1; 93:2; 102:1); its entrance into the oralo-branchial chamber lay in the first branchial fossa immediately ahead of the first gill-sac near the groove *pbg* (fig. 15; pls. 27:2; 29:2; 30:1) or somewhat more posteriorly (pls. 13; 17), or in many forms rather far forwards. In some cases (pls. 30:1; 108—109) it or one of its branches entered the oralo-branchial chamber closely behind the velar ridge, went forwards in a groove in the roof of the chamber and pierced the velar ridge in order to enter into the tissues of the oral cavity. In several species (and most distinctly so in *C. signata)* the proximal course of its branches or, probably more exactly, some of its branches could be traced by grooves in the roof of the oralo-branchial chamber in which they were lodged immediately after they had left their canals in the endoskeleton. The distal course of the nerve branches is unknown as well as the place of their termination, and the nature of the different branches can thus not be determined. In the oralo-branchial chamber the r. maxillaris, however, most probably supplied the oral muscles (and possibly also some of the velar muscles), and sent branches to the mucosa in the mouth cavity. The nerve must thus have been composed of visceral motor and somatic sensory (general cutaneous) fibres (there were most probably no visceral sensory fibres associated with it).

The r. mandibularis or the posterior pure motor trunk of the n. trigeminus (V_3) took its exit from the cavum cerebrale through the most anterior part of the fenestra (canalis) acustica, and passed through the antero-median part of the labyrinth cavity, sometimes in a distinct groove in the wall of this cavity. It left the labyrinth cavity in a canal of its own which either opened into the posterior part of the orbit or continued uninterrupted outwards through the orbito-temporal region of the endocranium into the visceral endoskeleton (fig. 12; pl. 112:1). In the former case the nerve traversed the postero-lateral part of the orbit, lying in a groove in the floor of the orbit or in any case near this floor. It left the orbit and was, during its passage to and in the visceral endoskeleton, lodged in the canal V_3 (pls. 3:2; 8:2; 10:2; 61; 62:1; 63:2; 68:3; 69:1; 70; 71:2; 78:3; 86:2; 89:2; 91:2; 93:2; 94—95; 97:1, 3; 100:1; 102:1; 103:4; 106—109). It entered the oralo-branchial chamber by one or two branches in the dorso-median or in the ventro-lateral part of the (anterior half of the) second branchial fossa, and it or its branches produced one or several fine grooves in the roof of the oralo-branchial chamber, leading from the most anterior part of the second branchial fossa to or over into the first branchial fossa. The opening of the canal (or canals) for the r. mandibularis into the oralo-branchial chamber (and often also the grooves for the nerve in the roof of this chamber) is seen in pls. 9:6-7; 13—14; 16:1; 27; 29:2; 78:2-3; 81:2; 82:1; 83; 85; 87:1; 91; 93:1; 94:2; 95—96; 108—109; 110:1; (in this connection it can be observed that most of the branches of the groove for the r. mandibularis in a *Kiaeraspis* specimen, figured by Stensiö, 1927, fig. 36; pl. 51, V_2, had most certainly not lodged any nerve branches). The r. mandibularis innervated muscles in the wall of the first (spiracular or mandibular) gill-sac in the region in front of the first gill-opening and probably also other deep lying (branchial, pharyngeal and velar) muscles.

The n. trigeminus in the Osteostraci had already lost much of its presumed simple and primitive nature, and had been much transformed and specialized in comparison with the following typical branchial nerves VII—X, but it was certainly not so elaborately developed as the n. trigeminus in modern Cyclostomes with which it, however, showed several important resemblances (cf. pp. 63, 66, 70, 71, 75).

With regard to the n. abducens (VI) very little can be said. It probably emerged from the cavum cerebrale in company with the motor trigeminus roots but whether it left the cavum in a canal of its own (? *Vma,* fig. 10; pl. 57:2-3) or in a canal together with the trige-

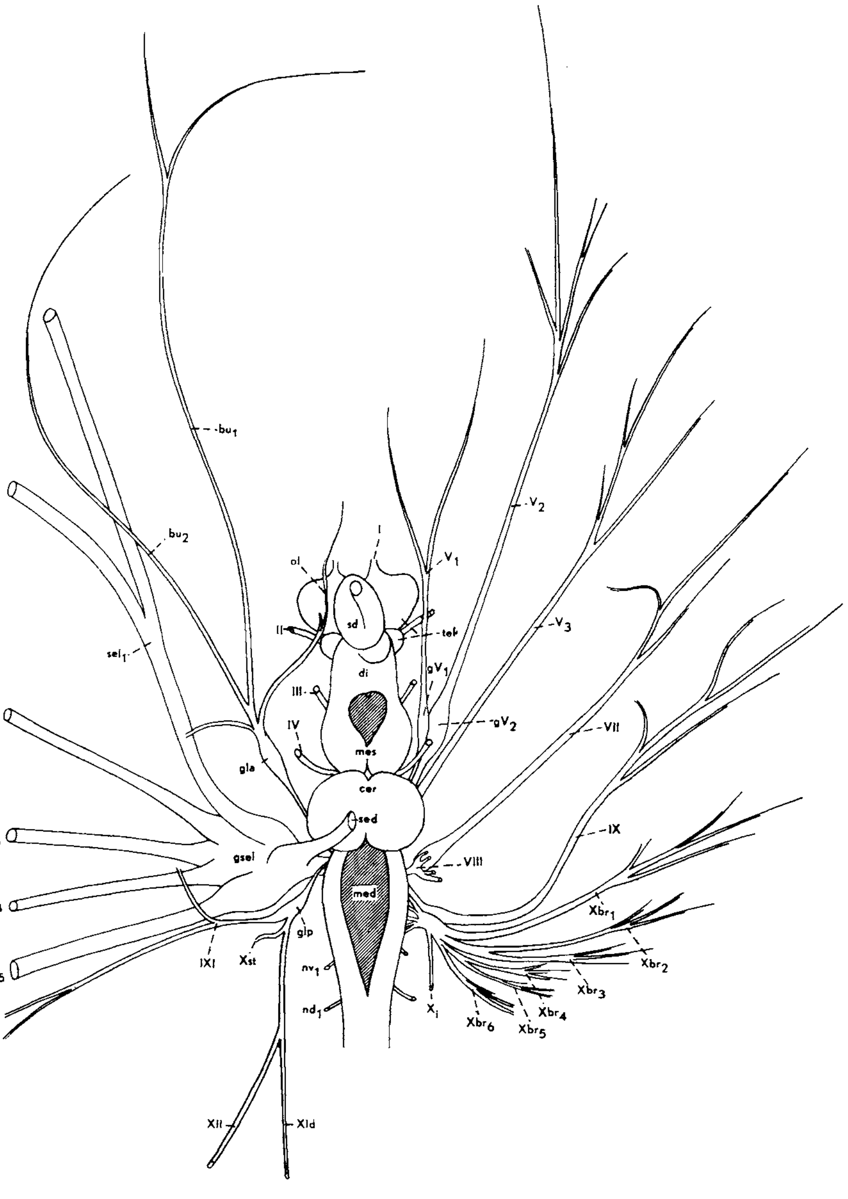

Fig. 20. — *Cephalaspis.* Attempted reconstruction of the brain and the cranial nerves (based mainly on the conditions in *C. signata).* To the right the ordinary nerves (cutaneous branches except n. profundus omitted), to the left the nerves for the sensory fields and the lateralis nerves. Dorsal view.

bu$_1$, *bu*$_2$, anterior and posterior divisions of the r. buccalis; *cer,* cerebellum; *di,* diencephalon; *gla,* ganglion of the n. lateralis anterior; *glp,* ganglion of the n. lateralis posterior; *gsel,* ganglia of the nerves for the sensory fields; *gV*$_1$, profundus ganglion; *gV*$_2$, ganglion gasseri; *mes,* mesencephalon (tectum opticum); *med,* medulla oblongata; *nd*$_1$, dorsal root of the first spinal nerve; *nv*$_1$, ventral root of the first spinal nerve; *ol,* r. ophthalmicus lateralis; *sd,* saccus dorsalis; *sed,* nerve for the dorsal sensory field; sel_{1-5}, nerves for the lateral sensory field; *tel,* telencephalon; *I,* n. olfactorius; *II,* n. opticus; *III,* n. oculomotorius; *IV,* n. trochlearis; V_1, n. profundus (r. ophthalmicus trigemini); V_2, r. maxillaris trigemini; V_3, r. mandibularis trigemini; *VII,* n. facialis; *VIII,* n. acusticus; *IX,* n. glossopharyngeus; *IXl,* lateralis branch accompanying the n. glossopharyngeus; Xbr_{1-6}, branchial rami of the n. vagus; *Xld,* lateralis branch for the dorsal lateral line; *Xi,* r. intestinalis vagi; *Xll,* lateralis branch for the main and the extra-lateral lines; *Xst,* lateralis branch for the supratemporal sensory line.

minus roots *(Vm)* cannot be made out; in any case the nerve entered the trigeminus-lateralis chamber through the canal *Vm* and then passed on to the orbit.

The n. facialis (VII) issued with its root fibres from the cavum cerebrale through the fenestra acustica in company with the r. mandibularis V and the roots of the nerves for the sensory fields and of the n. acusticus, and entered the labyrinth cavity; probably soon within this cavity some of its fibres became ganglionic and formed the facialis ganglion (g. geniculi) which probably lay in the ventromedian part of the vestibulum. The nerve, issuing from it, went through the vestibulum and emerged from it in the canal *VII* between the canals sel_1 and sel_2 (cf. pl. 32:1). It is interesting to note that in *Petromyzon* the roots of the n. facialis enter the labyrinth cavity, and that its ganglion is intra-capsular (Johnston 1902a, p. 45; 1905a, pp. 157—159, 163; Tretjakoff 1927a, p. 402; Cords 1929, pp. 229—231; Lindström 1949, p. 385). Some superficial canals are considered by Stensiö (1927, pp. 160, 194) to have been canals for general cutaneous branches of the n. facialis but in the present material no superficial canals could be attributed with certainty to this nerve (cf. p. 127). It seems, however, very problable that such fibres really were present in the n. facialis of the Osteostraci as they are present in recent Cyclostomes (Johnston 1905a, pp. 185, 198; Jansen 1930, pp. 449, 455) and, although rather seldom, also in fishes (Kingsbury 1897, p. 8; Kappers 1914, pp. 103—104; Norris 1925, p. 358; Horst 1928), forming an integral part of this nerve (and thus not only present in branches which peripherally unite with it, as in several Teleosts, cf. Herrick 1899; 1900; 1901; Rutkiewicz 1921). After a short *(Cephalaspis)* or long passage through the visceral endoskeleton in the canal *VII* the n. facialis entered the oralo-branchial chamber (cf. figs. 12, 14—15; pls. 10:2; 14; 15:1; 27; 29:2; 32:1; 61; 71:2; 77:2; 81:2; 82:1; 83:2; 85; 86:2; 87:1; 91:1; 93; 94:2; 95—96; 100:1; 103:1; 106—109, in which the canal *VII* or the opening of it into the oralo-branchial chamber is seen) in the second (pls. 27:1; 85; 86:2; 87:1) or third branchial fossa (pls. 14; 15:1; 27:2; 93:1; 94:2; 96) as a common trunk or after having, during its passage through the endoskeleton, divided into two or three branches. The nerve, or its branches (or some of its branches), during its proximal course in the oralo-branchial chamber, produced impressions in the roof of this chamber in form of grooves, and these grooves continued over into the roof of the second branchial fossa in case the nerve had entered behind the second interbranchial ridge (thus in the third fossa). In a well preserved specimen of a *Cephalaspis* species *(C. signata,* pls. 27:2; 29:2) grooves, interpreted as grooves for four branches of the n. facialis, are present, and it is of considerable interest to note that grooves for corresponding branches with similar disposition, belonging to the n. glossopharyngeus and some of the branchial rami of the n. vagus, have also been observed. To judge from the course of these branches the n. facialis supplied branchial muscles in the wall of the second gill-sac or in the region between the second and third interbranchial ridges or in the area lying morphologically between the first and the second branchial openings; it thus went down to the branchial region behind the first branchial opening and behind the hyoidean visceral arch to which it belongs. The n. facialis was a typical branchial nerve, and was composed of visceral motor, (probably) somatic sensory and (most probably) visceral sensory fibres. None of the grooves for the facial branches can be assigned with certainty to a special r. visceralis, but possibly the most median branch, in the groove *VIIa,* may have represented such a ramus.

In connection with the n. facialis we must consider the nerves for the sensory fields as they formed most probably a specialized part of the n. facialis or, more specifically, possibly were a transformed part of the lateralis element, associated with the facialis-acusticus complex. The roots of these nerves went all through the fenestra acustica and became ganglionic in the labyrinth cavity; here they formed several ganglia, probably one for each nerve of the lateral field (or fields), and one for the nerve of the dorsal field. The ganglia for the former nerves were situated on the floor of the vestibulum in which they formed in some cases marked impressions or were lodged in partly separated compartments (pls. 3:1; 16:1; 81:2; 83:1; 94:2). In one *Cephalaspis* species *(C. signata,* pls. 31:1-3; 32:1-2) the ganglion of the first nerve for the lateral sensory field was situated in the most proximal widened part of the nerve canal. The position within the labyrinth cavity of the ganglion of the nerve for the dorsal field is unknown. The nerves which issued from the ganglia went in two directions, the single nerve for the dorsal sensory field running upwards to this field, and the remaining nerves mainly in lateral direction. The five (very seldom six, in a specimen of *Boreaspis macrorhynchus)* nerves which constituted this latter group left the lateral part of the vestibulum, each in a canal of its own *(sel_1—sel_5,* seen in many of the plates) and went in centrifugal, radiating direction on to the lateral sensory field (or fields). In the Cephalaspids proper the anterior one of these nerves went in a canal *(sel_1)* from the vestibulum in anterior and slightly lateral direction to the postero-lateral corner of the orbit, followed the dorso-lateral margin of it forwards and, near the antero-lateral corner of the orbital opening, turned in antero-ventro-lateral direction, entering the visceral endoskeleton. At this point it divided into two main branches (most of the *Cephalaspis* species) or the bifurcation took place more distally, between the orbit and the lateral sensory field *(Securiaspis, Tegaspis, Benneviaspis, Hoelaspis, Ectinaspis)* but in other cases (exceptionally in *Cephalaspis,* in *Boreaspis, Kiaeraspis, Axinaspis, Acrotomaspis, Nectaspis)* the nerve did not bifurcate but continued as a main trunk which in the lateral field or just medially to it broke up into its terminal branches. In those forms in which the lateral sensory field was subdivided into two, three or four portions, the first field received the first *(Acrotomaspis)* or the first and second nerves *(Axinaspis, Nectaspis,* occasionally in *Kiaeraspis* and *Boreaspis);* if only two fields were developed the posterior one received the third to fifth nerves *(Axinaspis,* occasionally in *Kiaeraspis* and *Boreaspis);* the second field received in *Nectaspis* the third and fourth nerve but in *Acrotomaspis* only the second one. The third field in *Nectaspis* was supplied by the fifth nerve and in *Acrotomaspis* by the third nerve and the fourth field in *Acrotomaspis* by the fourth and fifth nerves.

The nerves for the lateral sensory field were regarded by Stensiö (1927, p. 196) as having a "metamerical" disposition but I cannot find that they alternated with the ordinary branchial nerves in such a way, and regarding their supposed development from the acustico-facialis complex I believe it highly improbable, that they could have a segmental origin.

The nerves for the sensory line system were in the Cephalaspids, as far as known, developed as a preauditory (prootic) n. lateralis anterior and a postauditory (metotic) n. lateralis posterior. As in recent Cyclostomes (Johnston 1905a; Worthington 1906; Holmgren 1919; etc.) the n. lateralis anterior (partly corresponding to the n. buccalis in *Petromyzon)* had an independent position in relation to the n. facialis, and its ganglion was (as in the Myxinids) situated closely to the ganglia of the n. trigeminus. The root fibres of the n. lateralis anterior, after their exit from the medulla oblongata, ran forwards in the cranial cavity, in some cases in a groove in the lateral wall of the cavum cerebrale, dorsally to the fenestra acustica, and left the cavity through the canal *lat* (fig. 10; pls. 14; 15:1; 17; 31:1; 57:2-3). They entered the trigeminus-lateralis chamber and formed a ganglion in the antero-lateral part of this chamber (possibly in some cases partly reaching into the orbit), lying laterally to the trigeminus ganglia. The nerve fibres which arose from this ganglion and which probably were not collected into distinct nerve trunks can be divided into two groups, a dorsal and a lateral. The former group, the fibres of which can be combined under the name of n. (or ramus) ophthalmicus lateralis, went in dorsal direction within the median part of the orbit and then in narrow canals (the course of which has not been wholly made out) to the neuromasts in the anterior and posterior portions of the supraorbital line (cf. pl. 15:2, *su*). The lateral group to which the term n. (r.) buccalis is applied, went in separate bundles along the floor of the orbit, often in distinct grooves in this floor (pls. 8:2; 14; 15:1), and left the orbit in narrow canals which issue from its lateral part. In the superficial parts of the visceral endoskeleton the nerves went in canals of their own (cf. pls. 6:1; 12:5; 14; 16:2; 34:1; 36:1; 37; 38:2; 59:1; 60, *n, bu)* which in some cases soon joined the canals sel_1 (pl. 16:1) or V_3 (fig. 12; pl. 112:1) but in others were wholly independent. The nerve fibres of the lateral group innervated neuromasts in the anterior and posterior portions of the infraorbital line (and the anterior portion was innervated by a different branch than the posterior portion) and in the most anterior division of the main lateral line (the otical portion), and also probably those in the anterior marginal line.

The n. lateralis posterior had its ganglion (or ganglia) in the vagus canal where it lay closely adjacent to those of the n. glossopharyngeus and n. vagus. The nerve fibres from this ganglion (these ganglia) were associated proximally with the nerves mentioned but had on the whole a rather independent disposition. An anterior group of the fibres ran together with the n. glossopharyngeus in the canal *IX* and some nerve fibres probably followed the nerve in the canal IX_1 (fig. 11A—B; pls. 30:3; 31:1-2, 4-6; 32:1) in order to ascend to the superficial parts of the shield in the canals *n* (pl. 32:1) somewhat postero-laterally to the orbit. If these latter canals really transmitted lateralis nerve fibres, the fibres must have innervated neuromasts in the main lateral line and in the lines *cm* and *mp*. Other branches probably went through the canals *IXl (IXla, IXlp,* pls.15:1, cf. pls. 13—14, *n;* 31:4-6; 32:1; 39:1) and innervated neuromasts in a part of the main lateral line, in the scapular line, and probably also in the anterior portion of the extra-lateral line. The lateralis fibres which are assumed to have been associated with the n. vagus or, more exactly, constituted the r. lateralis vagi, issued from the vagus canal in posterior direction in the canal *Xl* (pls. 8:2; 14; 15:1; 17; 31:4; 39:1, 3) and soon entered the trunk cavity where they lay closely to the roof of this cavity, in some cases in grooves on the lower side of the interzonal endoskeleton. The main r. lateralis vagi divided into a branch which supplied the neuromasts in the dorsal lateral line and another branch for the neuromasts in the most posterior part of the main lateral line on the cephalic shield, and probably also in the main lateral line and the extra-lateral line on the scale-covered trunk division. The neuromasts in the line *stc* were without doubt innervated by a supratemporal lateralis branch of the n. vagus but no canal which can be interpreted as a canal for such a branch has as yet been discriminated.

The n. acusticus (VIII) entered the labyrinth cavity through the fenestra acustica but nothing definite can be said about the number and position of its ganglion (or ganglia) and the distribution of its nerve branches, whether there was one ganglion situated near the floor of the labyrinth cavity as in the Petromyzonts or two, situated closely to the medulla (thus intracranially and intrameningeally) as in the Myxinids (cf. Allis 1903a, p. 277; Worthington 1906, p. 172; Ayers & Worthington 1908, p. 10). Considering the shape of the labyrinth organ in the Osteostraci we can, however, assume that the n. acusticus on the whole was more similar to that in the Petromyzonts than in the Myxinids, and it is thus probable that it was not, as in the latter group, divided into two relatively independent parts (cf. Stensiö 1927, pp. 192—193) but that there was formed a single ganglion acusticum from which the nerve branches to the cristae anterior and posterior and to the different maculae in the labyrinth took their origin (cf. Tretjakoff 1907, pl. 2:5; Burlet & Verstegh 1930, fig. 19).

The n. glossopharyngeus (IX) was closely associated proximally with the n. vagus and the n. lateralis posterior. Its root fibres left the cavum cerebrale in the vagus canal, in which also the sensory fibres became ganglionic, and the n. glossopharyngeus then entered the canal *IX*. After probably having emitted branches with general cutaneous fibres in the canal *IXl* (together with lateralis fibres) the main nerve entered a canal (IX_1, figs. 11A—B, 12; pls. 15:1; 31:6; 32:1; 112:1) which in some species opens into the posterior part of the vestibulum but in others runs posteriorly and laterally to this cavity. In some forms the nerve thus ran behind and laterally to the labyrinth cavity *(Nectaspis,* some *Cephalaspis),* in others it pierced this cavity. Both conditions were present in the same genus *(Cephalaspis),* and the different disposition of the nerve in relation to the labyrinth cavity was thus not stabilized, and the question as to which of these different positions is primary and which is secondary appears to be of no importance in the Osteostraci (cf. the Selachians, Holmgren 1943, pp. 140—148). In the major part of its course through the endocranium the n. glossopharyngeus ran closely adjacent to the a. communicans. Posterolaterally and laterally to the vestibulum the nerve went across the fifth and fourth nerves for the lateral sensory field, and, after having given off some superficial branches (lateralis or general cutaneous, or, most probably, both) went down between the third and the fourth nerves for the lateral sensory field and entered the oralo-branchial chamber.

In the species in which the nerve traversed the labyrinth cavity it emerged from this cavity by a canal below the canal for the third nerve for the lateral sensory field and crossed this nerve on the ventral side. The opening for the nerve lies in the third or in the most anterior part of the fourth branchial fossa, in some cases *(Cephalaspis,* fig. 14; pls. 27; 29:2; 32:2) rather far dorso-medially or in the middle of the fossa, in others *(Boreaspis,* pls. 81:2; 83:2; 87:1) in its ventro-lateral part. In *C. signata* the n.glossopharyngeus had divided into two main branches just before it entered the oralo-branchial chamber, and in the roof of this chamber (in the anterior part of the fourth branchial fossa and in the third branchial fossa) are the grooves for the proximal parts of four of its branches, the anterior main branch having broken up into three secondary branches (in the grooves *a + IXa, IXb, IXc)* and the posterior main branch remained undivided (in the groove *IXd;* pls. 27:2; 29:2; fig. 14). These branches corresponded to similar branches of the n. facialis and the branchial rami of the n. vagus. The nerve supplied muscles between the second and third interbranchial ridges or in the area between the second and third branchial openings. It entered the branchial region behind the glossopharyngeal visceral arch (as in the Petromyzonts, cf. Alcock 1898, pl. 2:1, 3; Johnston 1905a, fig. 18; pl. 5). The n. glossopharyngeus very probably consisted of visceral motor, visceral sensory, and general cutaneous fibres, and was associated with a portion of the n. lateralis posterior.

The n. vagus (X), after the entrance of its root fibres into the vagus canal, formed a ganglion or, more probably, several ganglia in this canal. The main trunk of the nerve entered the canal *X* (fig. 11; pls. 8:2; 14; 15:1; 16; 30:3; 31:1-5; 32:2; 39:1, 3) and was either wholly or for the most part enclosed in a canal in the postbranchial wall, or the canal opened into the trunk cavity. In this case the nerve lay in a groove in the posterior side of this wall until it again pierced the wall either as a main trunk (pl. 39:3) or by several branches (cf. Stensiö 1927, pp. 54—55; fig. 14; pls. 84—85; 96) in order to reach the gill-sacs lying on the anterior side of the postbranchial wall. The branchial branches of the n. vagus will be described mainly after the conditions of its canals and grooves in *C. signata,* the only species in which they are known in any detail. The vagus trunk divided into three main branches (running in the canals Xbr_1, X_1, X_2, fig. 11B; pl. 31:4-6). The lateral one of these branches was the first r. branchialis vagi (in the canal Xbr_1, cf. also fig. 12; pl. 112:1); it entered the most posterior part of the fourth branchial fossa just postero-laterally to the otic prominence and into or near the groove for the a. branchialis efferens 4 (pls. 29:2; 35:3; cf. pls. 27:1; 81:2). It probably divided (before or after it had entered the oralo-branchial chamber) into several branches of which one (corresponding to the median branch of the nn. facialis and glossopharyngeus, in the grooves *VIIa* and *IXa*, respectively) ran in the canal Xbr_1a, and one (probably the common basal trunk for branches corresponding to the three lateral branches of the nn. facialis and glossopharyngeus) in the canal and groove Xbr_1 (pl. 35:3). The r. branchialis 1 vagi supplied i. a. muscles in the wall of the branchial sac between the third and fourth interbranchial ridges. The middle main branch of the n. vagus passed through a canal (X_1, fig. 11B; pls. 29:2; 31:4) which joins the canal for the a. subclavia on its postero-dorsal side. From the antero-ventral side of the same canal the vagus trunk went first in a canal in the postbranchial wall and then for a short distance in a groove on the posterior side of this wall; here it divided into two branches (cf. pl. 29:3). One of these branches, the second r. branchialis X, traversed the postbranchial wall together with the a. branchialis efferens 5 and entered the fifth branchial fossa (pl. 35:3, a_1X) in dividing in at least three branches (in the grooves *Xa, Xb, Xc,* pl. 35:3), corresponding to the three median branches of the nn. facialis and glossopharyngeus. The other branch, the third branchial ramus of the n. vagus, ran in a short groove on the posterior side of the postbranchial wall (Xbr_3, pl. 29:3; possibly, however, this groove gave passage to a basal stem consisting of more than one branchial ramus) and traversed this wall first in a canal together with the a. branchialis efferens 6 and, then, in a canal of its own; it opened into the sixth branchial fossa. The remaining branchial rami and a possibly present r. intestinalis vagi constituted the third main branch of the n. vagus which proximally ran in the canal X_2 (exposed in fig. 11B and pl. 31:4). These branchial rami must (in *Cephalaspis* and others) have been three in number; in the genus *Boreaspis* in which only seven branchial fossae and possibly only as many gill-sacs were present, possibly only four branchial rami of the n. vagus were formed in all. The r. branchialis 4 vagi must have gone down in the branchial fossa 7, behind the branchial opening 6 and supplied i. a. muscles in the wall between the interbranchial ridges (and septa) 6 and 7; the ramus 5 opened in the fossa 8, behind the opening 7, and supplied the area between the interbranchial ridges 7 and 8; the ramus 6 opened in the (last) fossa 9, behind the branchial opening 8, and supplied i. a. muscles in the region next behind the (last) interbranchial ridge 8. As there most probably were no gills on the posterior wall of the last branchial fossa (cf. Stensiö 1927, p. 170) there probably was no further ramus of the n. vagus developed behind the sixth one. Superficial canals for general cutaneous branches of the n. vagus have not been distinguished in the fossils but such fibres were beyond doubt present in the n. vagus in the Osteostraci. It seems very probable that the n. vagus with regard to its composition was built similar to the n. glossopharyngeus, and was thus composed of general cutaneous fibres and, in each branchial ramus, of visceral motor and visceral sensory fibres, and was accompanied by fibres from the n. lateralis posterior. It can be added that none of the branches now found in the n. vagus or in the other branchial nerves can be interpreted as a pretrematic branch (cf. Stensiö 1927, p. 165).

In the interpretation of the nerve canals in the Osteostraci, presented in this paper, the cranial nerves of the recent Cyclostomes could serve as a basis for the identification of the canals and cavities for corresponding nerves in the Osteostraci. With this proviso it can be said that the cranial nerves in this fossil group were in the main developed as in the modern Cyclostomes, showing resemblances to both the Petromyzonts and the Myxinids (the most notable exception is the development of the hypertrophied nerves for the sensory fields in the fossil group). And it is most important to observe that they had reached on the whole the same level of organization (with rather few primitive traits) as in the modern representatives of the group Agnatha. The Osteostraci are of little importance for the understanding of the changes which the nervous system had undergone in the early evolution of the vertebrates.

The vessels in the cephalic shield.

In this chapter, which contains a combination of the interpretations regarding the vascular canals in the shield of the Osteostraci, we shall mostly take into account only the normal conditions, excluding the disposition of canals, indicative of an aberrant development of the vessels, which not infrequently is met with, at least as to the vein canals.

The restorations in fig. 21A, B of the main arteries and veins, respectively, represent a generalized type of the vascular system in the shield of a *Cephalaspis* (and not the conditions in an actual species); they are hypothetical in several respects.

Arteries. — The heart lay probably closely behind the postbranchial wall, as assumed by Stensiö (1927, p. 204). The unpaired truncus arteriosus pierced this wall by a ventral foramen (*tr,* pls. 83, 85) of its own (probably, however, also serving as passage for the v. jugularis inferior) or passed through the ventral part of the common opening for the oesophagus and the truncus arteriosus *(oes + tr,* pls. 70:1; 99). In the oralo-branchial chamber the truncus very probably soon divided into two main branches (cf. recent Cyclostomes, Julin 1887, p. 772; pls. 21:1; 22:1; Jackson 1901, p. 20; fig. 10; Cori 1906, p. 15; fig. 3; Daniel 1934, pp. 319—320; fig. 4; etc.) which probably lay far apart and, on each side of the shield, in the lateral parts of the oralo-branchial chamber. Each of the branches of the paired truncus arteriosus gave off the afferent branchial arteries from the lateral side. These arteries went in the soft tissue ventrally to the interbranchial ridges and thus medially and internally to the visceral endoskeleton. It is noteworthy, however, that they ran so near to the endoskeleton that they in some cases left in it impressions in form of grooves (an a. branchialis afferens was thus in *C. signata* situated in the groove *aaff,* fig. 14; pls. 27:2; 29:2). The afferent arteries in each interbranchial ridge did not bifurcate but gave off small arterioles (cf. fig. 15; pls. 27:2; 29:2, *aaff?, aa)* to the gill-sacs in front of and behind the ridge.

The afferent arterioles were in the gills connected with the efferent arterioles which carried the oxygenated blood into the efferent branchial arteries. The many small efferent arterioles passed, like the afferent arterioles, from the posterior half of the gill-sac in front of and from the anterior half of the gill-sac behind the interbranchial ridge, and thus from the adjacent halves of two successive gill-sacs. They formed a series of anterior and a series of posterior arterioles which opened into the efferent branchial artery (as in the *Petromyzon* larva), and this artery ran as a main stem in the septum beneath each interbranchial ridge (the arterioles often ran in small grooves in the endoskeleton which forms the roof of the oralo-branchial chamber, cf. fig. 15; pls. 27:2; 29:2). The efferent branchial arteries ran, unlike those in recent Cyclostomes (cf. Julin 1887, p. 777; pl. 23:1; Cori 1906, p. 29; Hatta 1922, pp. 136—137; Daniel 1934, pp. 324—325) superficially in the branchial chamber and so closely to its roof that they often were located in grooves in the endoskeleton *(aeff,* figs. 14—15; pls. 27; 29:2; 32:2-3; 85; 87:1; 93:1; 94; 95:1; 108—109; 110:1). The efferent (and afferent) branchial arteries were thus closely related topographically to the visceral endoskeleton (contrary to what is the case in *Petromyzon,* cf., besides the authors cited above, also Tretjakoff 1927b, p. 256). The number of efferent arteries was nine in the genus *Cephalaspis* and others with nine gill-sacs. The anterior one of them, in front of the anterior gill-sac, was, however, slightly developed or, in comparison with the other following efferent arteries, reduced and transformed, and is counted as an efferent artery of its own. The number of real, wholly developed, efferent branchial arteries was thus eight.

The efferent artery in front of the first gill-sac is called the a. spiracularis (in the groove *asp,* figs. 14, 15C; pls. 27; 29:2; 109). The grooves for it are most elaborately developed in *C. signata,* and from the conditions in this species it can be inferred that the artery arose from small branches, arterioles, from the gills in the antero-dorso-median part of the first (the spiracular) gill-sac and emptied into the dorsal aorta. A small anterior branch in the dorsal region of the oralo-branchial chamber in the angle between the aortal ridge and the groove *pbg* must have been a nutritive artery.

Of the following efferent arteries, the aa. branchiales efferentes 1—8 (in the canals or grooves $aeff_1$—$aeff_8$), the first one arose from arterioles in the first (spiracular) and the second gill-sacs, and ran along the interbranchial ridge 1; the second efferent artery, along the interbranchial ridge 2, arose from arterioles in the second and the third gill-sacs; the third one, along the interbranchial ridge 3, arose from arterioles in the third and fourth gill-sacs; etc. The last one, the a. branchialis efferens 8, ran in the space between the branchial fossae 8 and 9 and was formed by the confluence of arterioles from the gills in the posterior half of the eighth and in the anterior half of the ninth gill-sac. It can be remarked that no canal or groove has been observed behind the ninth branchial fossa which could have transmitted an efferent artery behind the last gill-sac (and this gill-sac was thus most probably an incomplete one, bearing gills only in its anterior half; cf. Stensiö 1927, pp. 170, 179—180; cf. also the conditions in *Petromyzon* in which the last gill-sac is a complete one with an efferent artery behind it, Julin 1887, pl. 21:2; Cori 1906, fig. 1; Hatta 1922, pl. 22). The aa. branchiales efferentes 1—3 emptied into the aorta dorsalis. In *Boreaspis* also the fourth, and possibly the fifth, at least in some species, emptied directly into the dorsal aorta. The following efferent arteries (4—8) ran as follows (according to the conditions in *Cephalaspis,* the only genus in which they are fairly well known): The a. branchialis efferens 4 which ran along the fourth interbranchial ridge and arose from arterioles in the fourth and fifth gill-sacs joined the a. subclavia on its antero-ventral side (cf. fig. 11B; pls. 29:2-3; 35:3, $aeff_4$). The fifth efferent artery opened in *C. signata* medially to the fourth one and in the median continuation of the a. subclavia which now is called the a. (branchialis) efferens communis (par). In *C. exilis* this fifth efferent artery united with the a. subclavia rather far laterally, and the vessel arisen from the union of these arteries and running medially and receiving the efferent arteries 4 and 6—8 is called the paired a. efferens communis. The eighth efferent artery, in running in antero-dorso-median direction, joined the seventh efferent artery, and the artery arisen from this union received on its lateral side the sixth efferent artery (cf. pl. 27:1, $aeff_6$—$aeff_8$). The basal trunk for these three posterior efferent arteries then opened rather far medially into the paired common efferent artery (cf. pls. 27:1; 29:3). The paired a. efferens communis went in median direction and, in *Cephalaspis,* joined its fellow of the opposite side of the shield, forming a common unpaired vessel, the a. efferens communis impar, which was in communication with the aorta dorsalis. In *Boreaspis,* however, the paired common efferent artery opened separately and directly into the aorta.

The third efferent branchial artery communicated by means of the a. communicans with the a. segmentalis occipitalis.

The aorta dorsalis, having originated from the confluence of the aa. branchiales efferentes, had its anterior end at the union of the aa. spiraculares; it reached thus far anteriorly in the head. Its forward extension is, however, somewhat variable, being different in different species (cf. the position of the groove *asp* in pls. 27:1; 29:2; 109). The aorta was an unpaired vessel throughout its length. It ran dorsally just beneath the roof of the oralo-branchial chamber (often in a distinct groove, *ao,* seen in figs. 14, 15; pls. 17; 27:1; 30:3; 31:1-2; 38:1; 85; 86:2; 87:1; 93:1; 94; 96; 106; 108—109), pierced the postbranchial wall in its dorso-median part (pls. 3:1; 27:1; 70:1; 81:1; 83; 84:2; 85; 86:2; 94; 99), and was behind this wall situated in a very wide groove in the ventral side of the inter-zonal endoskeleton and distinctly on the right side of the median line (seen in pls. 3:1; 8:2; 13—14; 15:1; 17; 32:2, 4; 33:1; 39:1, 3; 56:1).

Forwards from the point of its origin by confluence of the spiracular arteries the aorta was continued by an unpaired median vessel, the a. rostralis (impar), a nutrient artery for the rostro-median parts of the shield. The a. rostralis went forward for a long or short distance immediately below the "aortal" ridge, in some cases in a groove on the ventral side of this ridge (cf. fig. 15). In *Kiaeraspis* the rostral artery was paired right from its origin (cf. Stensiö 1927, pl. 51, *a. rostr).* In *Nectaspis* (fig. 15C; pls. 108—109) in which the aorta reached almost as far as to the velar ridge the unpaired a. rostralis was enclosed in a canal in this ridge and during its passage through it the artery bifurcated, forming the paired a. rostralis. In this genus a pair of arteries, the a. velaris, took its origin from the aorta at the transition to the a. rostralis or possibly as a branch of the a. spiracularis and went downwards to the velum (cf. fig. 15C; pls. 108—109, *av).* The unpaired rostral artery sent small branches to the dorso-median region of the roof of the oralo-branchial chamber in front of the first gill-sac near the aortal ridge (pl. 29:2, *ard).* Anteriorly it bifurcated in giving rise to a paired vessel (a. rostralis par) which ran in the roof of the mouth cavity (pl. 27:1; cf. pl. 9:6; pls. 29:2; 30:1, *arostr),* and in some species it entered a canal in the most rostral part of the visceral endoskeleton (figs. 14; 15A, B; pls. 29:2; 78:2; 87:1). In *Boreaspis* with a well developed rostral process, the a. rostralis supplied this process (running in a longitudinal canal, cf. pls. 79:2; 87:2, *rostrv).* In a canal in the rostral part of the ventral rim or in a grove in the roof of the buccal area the paired a. rostralis passed over into the a. marginalis (cf. pls. 9:6; 27:1). From the rostral artery or from the most anterior part of the marginal artery small superficial arteries issued supplying the dorsal (and ventral) outer parts of the rostral portion of the head (in the canals *ars,* pls. 8:1; 16:2; 34:1; 38:2).

The long extent forwards in the head of the aorta dorsalis and the development of an anterior continuation, the a. rostralis, from it was a feature peculiar for the Osteostraci, not found (normally) elsewhere (cf., however, the peculiar pre-branchial development of the arterial system in the Myxinids, Jackson 1901; Cole 1925; Grodzinski 1926; Holmgren 1946, pp. 57—70).

The paired carotid artery (a. carotis) ascended from the dorsal aorta between the first and second (pl. 27:1), between the second and third (pls. 93:1; 94:2; 108—109) or between the third and fourth efferent arteries (pl. 86:2) but its origin lay always beneath the ethmoidal region of the endocranium. The a. carotis generally entered the ethmoidal division of the cranial cavity (figs. 10, 12; pls. 4:2; 8:2; 14; 15:1, 3-4; 16—17; 83:1-2; 86:2; 94:2; 112:1, *acar)* but in *Kiaeraspis* it went in a canal wholly outside of this cavity (cf. Stensiö 1927, p. 208; pl. 55). It soon, and usually within the ethmoidal cavity, divided into two branches, a median a. encephalica (anterior) and a lateral a. facialis (by Stensiö 1927, pp. 112, 208, homologized with the a. facialis in *Petromyzon,* "orbital artery", Daniel 1934; corresponding possibly to the a. oculo-nasalis in *Myxine,* cf. Towarnicki 1935). In some cases, however, the a. facialis arose directly from the aorta in front of the a. carotis (cf. pl. 15:3-4), and in *C. exilis* it (probably) left the a. carotis before this artery entered the ethmoidal cavity (cf. pl. 27:1).

The a. facialis ascended, first within the ethmoidal cavity and then in a canal of its own *(afac,* pls. 3:2; 4:1; 8:2; 14; 15:1; 17; 86:2; 109) in the endocranium towards the superficial parts of the ethmoidal region. During this passage the artery sent out several posterior and median branches (in the canals *afp* and *afm,* pls. 13; 15:2; 19:2; 36:1; 38:2; 106—109). Just before the facial artery reached the outer face of the endoskeleton it divided into an anterior and a strong lateral branch. The anterior branch is to be considered as the main a. facialis (cf. *Petromyzon,* Cori 1906, figs. 1—3, cf. Favaro 1908, fig. 45, Stensiö 1927, fig. 99; Tretjakoff 1927b, pp. 227—229; Daniel 1934, p. 326; fig. 9); it supplied the superficial parts of the head near the median line, anteriorly and antero-laterally to the nasal opening (cf. pls. 3:2; 4:2; 8; 10; 13; 15:2, 4; 23:1; 34:1; 36:1; 38:2; 62:1; 106, *afac).* The lateral branch which is called the a. adorbitalis (cf. pls. 3:2; 4:2; 8; 10; 13; 15:2; 23:1; 36:1; 38:2; 62:1; 106, *aad)* turned laterally and later postero-laterally and posteriorly and followed rather closely the anterior and lateral margin of the orbital opening, and ended near its postero-lateral corner. During its course the a. adorbitalis gave off several, and generally four, side-branches to the superficial region of the head in front of and antero-laterally to the orbit, between this and the lateral sensory field (but in some cases the branches reached over into this field, too); the branches passed in the canals *adl*$_1$—*adl*$_4$ (pls. 1:2; 6:2; 8; 10; 12:4-5; 13; 16; 23; 24:2; 25:2; 29:1; 36—38; 59:1; 62:1; 63:2; 69:2; 98:1; 106—107).

With regard to the a. encephalica anterior and its development in the Osteostraci nothing definite can be said, as the artery ran for the main part wholly intrameningeally without leaving any impressions in the wall of the cranial cavity. It must, however, have supplied the anterior parts of the brain, possibly also the olfactory organ (a. cerebralis anterior) as well as the eye (by a special branch, the optic artery, the a. ophthalmica magna Stensiö 1927, p. 212, the a. retinae centralis Allis 1931a, p. 153); probably a posterior branch, the a. cerebralis posterior, was developed, which possibly was in communication with the posterior encephalic artery (as assumed by Stensiö 1927, p. 212).

In the posterior part of the head, beneath the occipital region of the endocranium, the dorsal aorta gave off several important arteries.

The a. encephalica posterior (or occipitalis) generally issued directly from the dorsal side of the aorta, ascending in the canal *cpost* (pls. 9:7; 14; 15:1; 16; 39:1, 3; 57:2; 86:2; 112:1) and entered the cranial cavity. As seen from the conditions in *C. doryphorus* the a. encephalica posterior was probably the dorsal branch of the a. segmentalis occipitalis (cf. pl. 39:1, 3-4, *cpost, as).* The artery supplied the posterior parts of the brain and possibly in some species the dorsal side of the most anterior part of the medulla spinalis, probably also, the labyrinth cavity by a branch with went through the fenestra acustica (cf. *Petromyzon,* Tretjakoff 1927b, p. 225). Furthermore an artery, which probably was a branch of the a. encephalica posterior, went through the canal *dx* (pls. 13; 15:2; 29:3; 57:2-3) to the dorsal part of the otic region, possibly to the dorsal sensory field (cf. Stensiö 1927, pp. 215—216). Another artery which probably was a branch, or a direct continuation, of the a. encephalica posterior was the a. postorbitalis superficialis (in the canal *adsm,* pls. 8:1; 10:2; 11:4; 13; 15:2; 24:2; 30:3; 31:1-2; 36:2; 56:1; 57:2-3; 77:2; 106—107); this artery was assumed by Stensiö (1927, p. 212) to have been given off from the supposed a. encephalica communicans but, to judge from the conditions in *C. signata* (pl. 30:3), the artery must have run in a groove in the posterior wall of the division of the cranial cavity for the cerebellum and thus so far backwards that it seems highly probably that it really was in direct communication with the a. encephalica posterior. The a. postorbitalis superficialis supplied the outer dorso-median parts of the head, between the posterior parts of the orbits and postero-medially to them, thus i. a. the anterior part of the dorsal sensory field; some of its branches entered the posterior part of the orbit (pls. 30:3; 31:1-2).

The a. segmentalis occipitalis issued from the lateral side of the aorta dorsalis at about a transverse level with the origin of the vagus canal (cf. pls. 16:1; 30:3; 31:1-2, 4; 32:2, *as)* or behind this level (pl. 112:1), in a groove before or behind the postbranchial wall or in a canal in this wall. The conditions indicate in *C. doryphorus* that the basal trunk of the left occipital segmental artery and the left a. encephalica posterior issued from the aorta through the canal *cpost* (pl. 39:4). Rather soon the occipital segmental artery gave off an anterior branch, the a. communicans, which went in a canal *(acom),* lying closely adjacent to the canal for the n. glossopharyngeus (in some places the two canals fused) or in a common canal for the artery and the nerve. The a. communicans either passed posteriorly and laterally to the vestibulum (cf. figs. 11A-B, 12; pls. 30:3; 31:1-2, 6; 32:1; 112:1) or it traversed this cavity. In *C. excellens* the a. segmentalis occipitalis entered the vestibulum and the a. communicans branched off from this artery within the vestibulum (cf. pls. 15:1; 16:1). In the first case the a. communicans ran dorsally to the two posterior, the fourth and the fifth, nerves for the lateral sensory field and descended between the second and the third nerves, all outside of the vestibulum; in the latter case the artery left the vestibulum in a canal which issues from this cavity below the canal for the third nerve for the lateral sensory field; in both cases the artery, in *Cephalaspis,* opened into the a. branchialis efferens 3.

During its passage the a. communicans gave off small branches, the aa. vestibulares, to the wall of the vestibulum, a ventral artery to the dorso-median part of the oralo-branchial chamber (cf. pp. 96, 102, Stensiö 1927, pl. 28, *IXav),* and gave furthermore rise to the anterior dorso-lateral superficial arteries.

These arteries are usually four in number (in the canals *ala*$_1$—*ala*$_4$, pls. 6:2; 8:1; 10:2; 12:4-5; 13; 14:1; 16:2; 23; 25:2; 29:1; 36:1; 37; 38:2; 59:1; 60; 62:1; 63:2; 68:3; 106—108), seldom three or five (the last one in the canal *ala*$_5$, pls. 36:1; 37; 62:1). They took their origin from one or two basal trunks which issued from the a. communicans and ascended to the outer parts of the endoskeleton postero-laterally to the orbit, where they broke up into superficial arteries. These superficial dorso-lateral arteries radiated to the lateral parts of the shield, supplying the area lying laterally and postero-laterally to the orbit, between this and the lateral sensory field and behind the region of the lateral branches from the a. adorbitalis and before that the posterior dorso-lateral superficial arteries, or in the region traversed by the second—fourth nerves for the lateral sensory field.

A dorso-median artery (in the canal *ads,* pls. 106—107) in *Nectaspis* is possibly a dorsal branch from the a. communicans.

The main a. segmentalis occipitalis continued in lateral direction (pls. 31:1-2, 4-6; 32:1; 39:1, 3, *as),* and divided into two branches before it reached the outer part of the endoskeleton ventro-laterally to the posterior part of the dorsal sensory field (pl. 29:1, *alp);* in some species it traversed the vestibulum and left this cavity in its postero-lateral part (pl. 16:2, *alp).* It gave rise to the posterior dorso-lateral superficial arteries (in the canals alp_1—alp_2, pls. 13; 16; 29:1; 36—37; 68:3), two in number which supplied the posterior parts of the cephalic shield proper in front of the shoulder-girdle and antero-laterally to the inter-zonal part of the shield.

In some species of *Cephalaspis* or those with a well developed dorsal spine on the cephalic shield there was formed a special artery, the a. spinae dorsalis, which supplied this spine and other adjacent parts of the shield; in some species without a real dorsal spine there was a corresponding a. cristae dorsalis. The artery arose, as a paired vessel, directly from the aorta or there was possibly formed a common short basal stem for it and the a. encephalica posterior (in *C. doryphorus,* on the left side, also for the a. segmentalis occipitalis); it ascended from the aorta in the canal *cp* (pl. 33:1), *cpost* (39:1, 3-4) or *adspd* (pl. 31:2). In some species the root vessels which formed the artery ran in canals outside of the cavum cerebrale (pl. 33:1) or one of them ran in such a way while the other traversed the cranial cavity (pls. 29:3; 31:2), and in still other species the root vessels both entered the cavity. In all cases, however, these vessels encircled the medulla and united dorsally to it in the median line to form the unpaired a. spinae dorsalis (cristae dorsalis) which thus was formed dorsally to the cavum cerebrale (pls. 29:3; 33:1) or within this cavity, and in the latter case issued from the dorsal side of the cavum cerebrale or from the neural canal (pls. 15:2; 39:4; 56:1-2, 4; 57:3). The artery ran backwards, lying dorsally to the posterior part of the cavum cerebrale and to the neutral canal; during its passage it emitted several dorsal, lateral and ventral branches (cf. pls. 29:3; 32:4, *adspx;* 39:4, a_1, a_2; 56:4, a_1; see also fig. 13) to the dorso-median parts of the shield in front of the dorsal spine, including the posterior part of the dorsal sensory field, and to the neural canal. The a. spinae dorsalis either entered the dorsal spine as a main stem (cf. pls. 39:4; 40:1) or broke up into several branches (cf. fig. 13; pl. 56:4) of which all or only some supplied the dorsal spine. In *C. doryphorus* there was a second, posterior, artery for the dorsal spine which issued from the trunk division of the dorsal aorta (cf. fig. 6B; pl. 39:1, 4, *adspp).*

Vessels in the canals *aiz* (pls. 106—107) in the dorso-median region of the inter-zonal part of *Nectaspis* were probably arteries corresponding to the a. cristae dorsalis.

A segmental artery behind the occipital segmental artery must have issued from the trunk division of the dorsal aorta and went, partly in a groove *(asb,* pls. 13—14) in the ventral side of the interzonal endoskeleton, in the roof of the most anterior part of the trunk cavity, on to the shoulder-girdle. Here the artery ascended to the outer parts of the endoskeleton and gave rise to the aa. scapulares (in the canals *asc,* asc_1—asc_3, figs. 16—17; pls. 6:2; 8:2; 12:4-5; 13—14; 18:1; 36—37; 59:1; 60; 77:2) which supplied the dorsal side of the shoulder-girdle proper.

The a. subclavia took its origin from the paired a. branchialis efferens communis and went in a canal in the postbranchial wall *(asubcl,* pls. 27:1; 29:2-3; 31:4-6; 40:2; 70:1; 85; 86:2; 97:3; 99:2; 110:2) towards the shoulder-girdle (lying, at least in *Cephalaspis,* above the interbranchial ridge 5). After having reached this part of the shield the a. subclavia turned rather abruptly in lateral or antero-lateral direction and ran behind the large marginal vein sinus to a point near its postero-lateral corner, in the base of the cornu (in species in which this part was developed), where the artery bifurcated and passed over into the anterior a. marginalis and the posterior a. cornualis. During its passage through the postbranchial wall the a. subclavia gave off several branches to the posterior side of this wall (cf. pls. 29:3; 31:4-6, *apw, apwd, apwv)* and farther outwards superficial branches ("r.superficialis ventralis of the a. subclavia", Stensiö 1927, p. 217) to the ventral side of the shoulder-girdle proper (cf. pl. 29:2, *avs* and Stensiö 1927, fig. 40; pls. 109—112, *a. vs).* Behind the median part of the marginal vein sinus the a. subclavia emitted, in posterior direction, the a. brachialis for the pectoral fin; this artery ran in a canal which in some species, closely before it opened into the pectoral sinus, divided into two branches *(abr,* abr_1, figs. 16—18; pls. 12:5; 18:1; 28:2; 30:2; 40:3; 85; 86:2; 110:2). In *Axinaspis* the a. subclavia gave off one posterior and one anterior a. brachialis (fig. 19; pl. 98:2-3, abr_1, abr_2); in this species the posterior part of the pectoral fin (or the posterior part of the pectoral area) was probably supplied by an additional artery, a branch from a segmental artery (fig. 19; pl. 98:3, *a).*

The a. cornualis (cf. figs. 17—18; pls. 12:5; 18:1; 28:2; 97:3, *ac)* ran to the ventral side of the distal half of the cornu and sent out (in some species) an anterior branch (in the canal *acant,* fig. 17; pl. 18:1) to this side of the basal half of the cornu. From the a. marginalis an additional cornual artery emerged, going to the lateral part of the cornu (a. cornualis accessoria, cf. fig. 17; pl. 18:1; 97:3, *aca).*

The a. marginalis ran forwards from its origin in the antero-median part of the cornu along the lateral margin of the shield between this margin and the v. marginalis, enclosed in a canal *(amarg,* pls. 9:6-7; 27:1; 29:2; 30:1; 97:3; 108—109). During its forward course it gave off numerous superficial branches (in the canals *ams,* pls. 37; 60) and also some branches to certain structures close to the external ducts from the gill-sacs (pl. 27:2, *a*) and gradually decreased in size so that anteriorly it was a very narrow vessel (pls. 9:6; 27:1). In the rostral part of the shield the a. marginalis divided into two branches, and was, by means of the median one of them, in communication with the rostral artery; the lateral branch (and the main a. marginalis) probably emitted some superficial arteries to the dorsal side of the most rostral part of the shield (cf. pls. 8:1; 16:2; 34:1; 38:2, *ars*).

We have already mentioned that the a. communicans gave off a ventral branch to structures in the dorso-median part of the oralo-branchial chamber. Similar arteries also issued from the unpaired a. branchialis efferens communis (cf. p. 152; Stensiö 1927; fig. 33; pls. 106—108, $a.eff_4$—$a.eff_6$). They were comparable to visceral side-branches of the dorsal aorta in *Petromyzon* (Favaro 1908, p. 375), in *Myxine* to the median aa. nutritiae branchiales from the efferent branchial arteries and to nutrient arteries (to the pharynx) from the prebranchial part of the lateral aorta (Grodzinski 1926, pp. 131, 134), and to the aa. nutritiae branchiales (dorsales) which in fishes issue from the efferent branchial (epibranchial) arteries (Parker 1886, p. 698; Allen 1905, p. 62; pl. 1:1, cf. 1907, p. 107; Silvester 1905, pp. 96, 100—102; Allis 1912, p. 483; Burne 1924, pp. 227—230; O'Donoghue & Abbott 1928, p. 851; etc.).

The most posterior part of the canal *aeffc* (pl. 27:1; 99:2) which pierces the postbranchial wall transmitted a posterior branch (or posterior branches) of the unpaired a. branchialis efferens communis, and this branch must have been a nutrient artery (arteries) for structures in the (anterior part of the) trunk. In *Boreaspis* a probably paired artery issued directly from the aorta (in the canal *apns*, the groove *apnd* and through the opening *apn?*, pls. 85; 86:2; 94:2) and went (presumably) to the pronephros. In *Cephalaspis* a small paired artery which issued from the transition of the paired to the unpaired a. efferens communis probably supplied the pronephros (cf. Stensiö 1927, p. 245; figs. 35, 39—40).

Small dorsal arteries went from the aorta to the vagus ganglion complex (in the canals *a*, fig. 11C; pl. 31:4); and the posterior part of the cavum cerebrale and the anterior part of the neural canal were probably supplied ventrally by small irregularly disposed arteries from the aorta (they were thus not associated with the ventral nerve roots of the spinal nerves) and, dorsally, by branches from the a. encephalica posterior and the a. spinae (cristae) dorsalis. More posteriorly the neural canal as well as the dorso-median superficial parts of the shield (apart from the dorsal spine) were supplied by dorsal branches of segmental arteries (cf. fig. 13; pl. 56:1-3; *ads*, a_2—a_4).

Veins. — Canals and grooves in the cephalic shield for a possibly present lymphatic system cannot be distinguished from those of the venous system. As the existence of a lymphatic system has been prooved in both groups of the recent Cyclostomes (and as it thus is present in all groups of recent vertebrates) it seems not improbable that it was developed also in the Osteostraci. Possibly some of the sinus-like widened canals (e. g. the rostral vein sinus and the marginal vein sinus and the canal for the marginal vein) in the Cephalaspids had contained lymphatic vessels. It can be observed that the rostral vein sinus was regarded by Stensiö (1927, pp. 187, 227, cf. also p. 369) as exactly corresponding to an annular labial sinus in the Petromyzonts, and this sinus is now known to belong to an extensive system of lymphatic vessels in the anterior part of the head (cf. Hoyer 1938, pp. 4—22). It is to be mentioned that in the Cyclostomes the lymphatic system has been observed mainly in the adult forms and that almost nothing is known of its development (cf., however, Kurzmann & Paschma 1947). It seems rather probable that, if an independent lymphatic system existed in the Osteostraci, the relations between the lymphatic vessels and the veins were much closer than in the recent Cyclostomes. The so-called vein-canals in the Osteostraci are in fact readily interpreted as having transmitted veins, and if some of them may have contained lymphatic vessels also, these vessels probably were closely associated with and adjacent to veins. At the present time we can thus interpret canals for vessels other than arteries only as vein canals but with the reservation that some of them may have been canals for lymphatic vessels or had contained such vessels and veins.

The de-oxygenated blood in the cephalic shield of the Osteostraci was brought to the sinus venosus through two systems of veins, viz. that of the anterior cardinal veins (and possibly also the posterior cardinal veins) and that of the ventral jugular veins (v. jugularis inferior). Rather little is known of the deeply situated veins and the ventral superficial veins, and the main part of the following account thus refers to the superficial veins of the upper side of the cephalic shield.

To the system of the cardinal veins belonged *a,* the v. capitis lateralis and its tributaries, the superficial dorso-lateral and dorso-median veins and the anterior cerebral vein, *b,* (as a transformed tributary of the v. capitis lateralis) the occipital vein sinus and veins from the otical region, the superficial occipital and inter-zonal veins, the v. cerebralis posterior and the anterior transformed vertebro-medullar veins, all emptying into the sinus, *c,* some posterior vertebro-medullar veins and other dorsal branches of segmental veins which probably discharged into the posterior cardinal veins. To the system of the ventral jugular veins (v. jugularis inferior) I refer here *a,* the marginal vein and its branches, including i. a. the veins from the shoulder-girdle and those from the pectoral fin, as well as some more deeply situated veins from the branchial region, *b,* the rostral vein and its superficial branches, and *c,* veins in the roof of the oral cavity which emptied directly into the v. jugularis inferior.

The anterior, cephalic, division of the anterior cardinal vein was the v. capitis lateralis. It originated in the superficial part of the ethmoidal region and the area immediately in front of it, and drained here the area supplied by the a. facialis (cf. pls. 6:2; 8:1; 10; 15:2; 16:2; 19:2; 23; 29:1; 36:1; 37; 38:2; 62:1; 63:2; 67:1; 71:2; vcl_1). It ran in posterior direction and descended gradually into the endoskeleton, and finally pierced (cf. pls. 3:2; 4:1; 77:2) the anterior wall of the orbit. This vein was certainly, as assumed by Stensiö (1927, p. 118) the initial branch of the v. capitis lateralis, and it cannot have been homologous with the v. facialis in the *Petromyzon* larva, as suggested by Lindström (1949, p. 446). Well within the orbit the v. capitis lateralis must have run near the median (interorbital) wall of the orbit (and not along the lateral wall as in the restorations by Denison 1951a, figs. 22—23), and passed out through the postero-dorsal or postero-dorsolateral wall of the orbit. From the orbit it went, straight or sigmoidally bent, in posterior direction, lying dorsally to the lateral part of the vestibulum or traversing this cavity (cf. pl. 93:2, *vcl*). The canal *(vcl)* for this part (the postorbital division) of the v. capitis lateralis is seen in many specimens (pls. 5:3; 8:1; 10; 11:4; 13—14; 15:1-2; 16—17; 30:3; 31:1-2, 4; 32:1, 3; 33:1; 39:1, 3; 56:1; 62:1; 63:2; 64:2; 68:3; 77:2; 93:2). Postero-laterally to the labyrinth cavity and after having crossed the posterior nerve for the lateral sensory field on the dorsal side, it went deeper into the endoskeleton and emerged from the endocranium, entering the most anterior part of the trunk cavity of the shield. Here it must have turned medially and somewhat ventrally and joined the v. cardinalis posterior at the end of the ductus cuvieri (the conditions, however, possibly differed from this general plan in as much as the proximal parts of the vein trunks had already in the Osteostraci been subjected to some transformation and asymmetrical development; cf. the recent Cyclostomes, Jackson 1901; Vialleton 1903; Goodrich 1930, pp. 543—544; etc.).

The v. capitis lateralis in the Osteostraci was undoubtedly (partly) homologous with the vein with this name in the Cyclostomes (in *Petromyzon* also called the v. jugularis superficialis) and fishes, as pointed out by Stensiö (1927, pp. 74, 230). The anterior continuation of the v. cardinalis anterior was thus in the Osteostraci formed by the v. capitis lateralis, and already in these old forms the v. capitis medialis had yielded place to this vein. It is thus of interest to notice that very early in the ontogenetic development of *Petromyzon* the v. capitis medialis disappears and is replaced by the v. capitis lateralis (Grosser

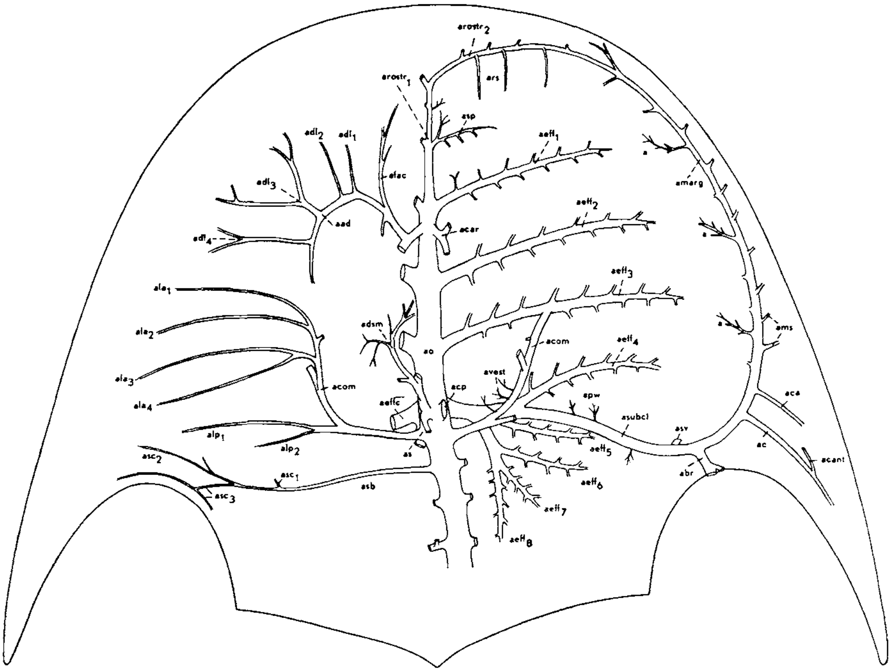

Fig. 21A. — *Cephalaspis.* Attempted restoration of the main arterial vessels in the cephalic shield (diagrammatic and generalized conditions). The truncus arterious and its branches omitted. To the right mainly deeper situated arteries as well as the rostral and marginal arteries, to the left the superficial arteries of the dorsal side of the shield (except the superficial marginal and rostral vessels). Dorsal view.

a, branch from the a. marginalis to a structure near the external branchial ducts; *aad,* a. adorbitalis; *abr,* a. brachialis;*ac,* a. cornualis; *aca,* a. cornualis accessoria; *acant,* anterior branch of the a. cornualis; *acar,* a. carotis; *acom,* a. communicans; *acp,* a. encephalica posterior; *adl*$_1$—*adl*$_4$, lateral branches of the a. adorbitalis; *adsm,* a. postorbitalis superficialis; *aeff*$_1$—*aeff*$_8$, a. branchialis efferens 1—8; *aeffc,* a. branchialis efferens communis (par); *afac,* a. facialis; *ala*$_1$—*ala*$_4$, anterior dorso-lateral superficial arteries, 1—4; *alp*$_1$—*alp*$_2$, posterior dorso-lateral superficial arteries, 1—2; *amarg,* a. marginalis; *ams,* superficial branches of the a. marginalis; *ao,* aorta dorsalis; *apw,* branches from the a. subclavia to the postbranchial wall; *arostr*$_1$, a. rostralis impar; *arostr*$_2$, a. rostralis par; *ars,* superficial branches of the a. rostralis; *as,* a. segmentalis occipitalis; *asb,* segmental artery behind the a. segmentalis occipitalis; *asc*$_1$—*asc*$_3$, a. scapularis 1—3; *asp,* a. spiracularis; *asubcl,* a. subclavia; *asv,* ventral superficial branch from the a. subclavia; *avest,* aa. vestibulares.

1907, pp. 180—181; Gelderen 1924, pp. 546—548; the vein in older larvae of *Petromyzon,* by de Beer 1924, pp. 324—326, called the v. capitis medialis, is the v. jugularis profunda, a visceral vein according to Gelderen).

The v. capitis medialis, as an independent vein, was absent in the Osteostraci but possibly some parts of the v. capitis lateralis in the orbit and parts of the cerebral veins were remnants of this vein.

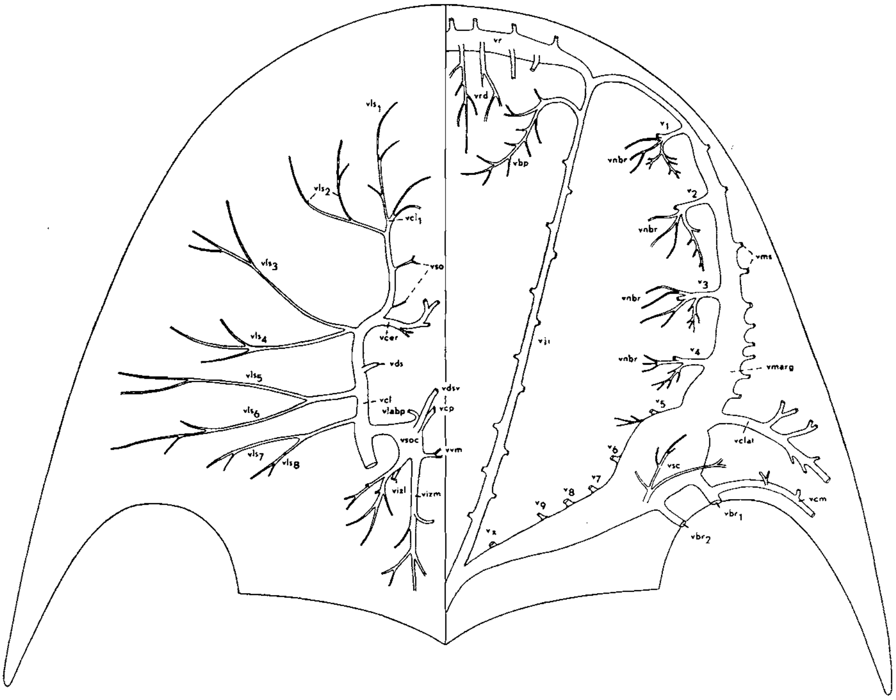

Fig. 21B. — *Cephalaspis.* Attempted restoration of the main veins of the cephalic shield (diagrammatic and generalized conditions). To the right the vv. jugularis inferior, marginalis and rostralis; to the left the v. capitis lateralis and its branches. Dorsal view.

v_1—v_9, vv. transversales ventrales, 1—9; *vbp,* v. bucco-pharyngealis; vbr_1—vbr_2, vv. brachiales; *vcer,* v. cerebralis anterior; *vcl,* v. capitis lateralis; vcl_1, preorbital division of the capitis lateralis; *vclat,* v. cornualis lateralis; *vcm,* v. cornualis medialis; *vcp,* v. cerebralis posterior; *vds,* dorso-median branch of the v. capitis lateralis; *vdsv,* v. oticalis; *vizl,* v. inter-zonalis lateralis; *vizm,* v. inter-zonalis medialis; *vji,* v. jugularis inferior; *vlabp,* v. posterior labyrinthi; vls_1—vls_8, vv. superficiales dorso-laterales, 1—8; *vmarg,* v. marginalis; *vms,* superficial branches of the v. marginalis; *vnbr,* vv. nutritiae branchiales; *vr,* v. rostralis; *vrd,* dorsal superficial branches of the v. rostralis; *vsc,* v. scapularis; *vso,* vv. supraorbitales; *vsoc,* occipital vein sinus; *vvm,* anterior v. vertebro-medullaris; v_x , hindmost ventral transversal vein.

If the Osteostraci had a vein corresponding to the v. jugularis profunda (v. cardinalis anterior, Cori 1906; Hatta 1922; v. capitis medialis, de Beer 1924) it must have run in the dorso-median part of the oralo-branchial chamber and emerged from this chamber through the dorso-lateral part of the opening in the postbranchial wall for the oesophagus or through the common opening for the oesophagus and the truncus arteriosus or, perhaps, through the aortal canal. Possibly the anterior continuation of this supposed vein was lodged in the groove *pbg* (pls. 13; 27:2; 29:2; 30:1; 36:2) and was connected with the v. jugularis inferior (this part of the vein would then have corresponded to the v. mandibularis in *Petromyzon,* cf. p. 136).

The most important of the superficial veins which drained the dorsal side of the cephalic shield proper were the dorso-lateral superficial veins, tributaries of the v. capitis lateralis. These veins drained a large portion of the dorsal side of the visceral part of the shield, anteriorly, laterally and postero-laterally to the orbit, reaching outwards to the median parts of the lateral sensory field. In the periphery of the shield superficial rostral and marginal veins were intercalated between the distal branches of the dorso-lateral superficial veins. The number of these latter was mostly six but in some cases seven or eight (the eighth vein was only developed as a branch of the seventh one). The two most anterior dorso-lateral superficial veins (in the canals vls_1, vls_2, pls. 1:2; 8:1; 11:4; 12:4; 15:4; 16:2; 19; 23; 29:1; 34:1; 36:1; 37; 38:2; 63:2; 67:1; 69:2; 71:2) generally opened into the preorbital division of the v. capitis lateralis (in a specimen of *C. excellens,* cf. pl. 15:4, the second vein united with the v. capitis lateralis within the orbit). The third to eighth dorso-lateral superficial veins (cf. vls_3—vls_8, pls. 1:2; 4; 6; 8; 10; 11:4; 12:4-5; 13—14; 15:2, 4; 16—17; 19:2; 23; 24:2; 25:1; 29:1; 31:1-2; 32:1-3; 36—37; 38:2; 59:1; 60; 62:1; 63:2; 64:2; 67:1; 68:3; 69:2; 70; 71:2; 77:2; 78:3; 90:3; 91:1; 93:2; 98:1; 100:1; 106—109) joined proximally in different ways so as to form two or three basal trunks by means of which they emptied into the v. capitis lateralis; never all of them were developed in one specimen as independent branches of this vein. The disposition of the proximal parts of the veins was in this way much diversified and often different in different specimens of one and the same species. The third dorso-lateral superficial vein or the basal trunk formed by this and the following vein (or veins) pierced the postero-lateral wall of the orbit and united with the v. capitis lateralis in the orbit (in most *Cephalaspis,* some *Securiaspis* and *Benneviaspis,* in *Ectinaspis)* or the union took place just at the point of exit of the v. capitis lateralis from the orbit (some *Securiaspis*), or at last, the vein emptied into the v. capitis lateralis behind the orbit and thus into the postorbital division of this vein (some *Cephalaspis* and *Securiaspis, Tegaspis, Hoelaspis, Boreaspis, Kiaeraspis, Axinaspis, Acrotomaspis* and *Nectaspis).*

The dorso-median superficial tributaries of the v. capitis lateralis were the supraorbital veins (cf. pls. 13; 15:2; 37; 38:2; 106—107, *vso, vsoa, vsop)* which drained parts of the interorbital region and emptied into the intraorbital division of the v. capitis lateralis, and furthermore small veins (cf. pls. 10:2; 37; 62:1; 106—107, *vds*) which joined the postorbital division of this vein coming from the region behind or postero-medially to the orbit and above the labyrinth.

The v. cerebralis anterior arose partly as a small superficial vein from the anterior part of the dorsal sensory field, partly as a real cerebral vein in the anterior part of the cranial cavity, which latter probably drained the dorsal side of the telencephalon, the diencephalon and the tectum opticum, possibly also an anterior part of the labyrinth organ (cf. fig. 10; pls. 8:1; 15:2; 33:1; 36:2; 56:1; 57, *vcer*). The main vein went down first entering the cavum cerebrale and running in this cavity and then issuing from it and passing in a canal outside of the cavum to the trigeminus-lateralis chamber or directly to the v. capitis lateralis just behind the orbit; in the former case the v. cerebralis anterior joined this vein in the postero-median part of the orbit. In the trigeminus-lateralis chamber the vein received a generally small tributary, arisen from two branches in the floor of the cavum cerebrale (cf. pl. 57:3, *v*), and which drained the lower part of the cranial cavity behind the dorsum sellae and also the ventral side of the midbrain (fig. 10; pls. 15:1; 57, *v*); this vein was homologized by Stensiö (1927, pp. 103, 228) with the v. pituitaria in fishes but the homologization is declined in this paper (cf. p. 77).

The occipital vein sinus *(vsoc,* only partly exposed in pls. 3:2; 10:2: 13; 15; 17; 56) was situated in a cavity (with the same name) in the endocranium behind or dorso-laterally to the labyrinth cavity and mainly within the occipital region of the endocranium. By a short vessel from its antero-lateral corner the sinus communicated with the v. capitis lateralis (cf. pls. 10:2; 17). A vein from the middle region of the dorsal sensory field, the otical vein, probably entered the canal *des* together with the nerve from this field, went in the canal *vdsv* (pls. 10:2; 13; 15:2; 57:2) which connects the canal *des* with the occipital vein sinus, and emptied into the antero-dorso-median part of the sinus (cf. Stensiö 1927, pp. 225, 230). In its antero-ventro-median corner the occipital vein sinus received the v. cerebralis posterior *(vcp)* which came from the posterior part of the cavum cerebrale (cf. pls. 17; 56:1-2) and entered the dorsal part of the vagus canal before it opened into the vein sinus through a very short canal of its own; in some cases, however, the v. cerebralis posterior went directly from the cavum cerebrale in a canal of its own (cf. pl. 56:2-3, in which in the same specimen both conditions are exposed). The v. cerebralis posterior probably drained the cerebellum and the medulla oblongata and received i. a. a v. posterior labyrinthi (in the canal *vlabp,* figs. 10, 11A; pls. 31:6; 57:2; cf. Stensiö 1927, pls. 25—26, *VIIIp)* from the posterior parts of the labyrinth cavity.

The dorsal side of the inter-zonal part of the cephalic shield was drained in some species by veins which emptied into two pairs of longitudinal superficial vein trunks. The lateral one of these, the lateral inter-zonal (superficial) vein *(vizl,* pls. 8:1; 10:2; 23:1; 29:1; 32:4; 33:1; 36:2; 39:4; 56:3; 59:1; 60; 62:1; 106—107), drained an antero-dorso-lateral region of the inter-zonal part or a lateral area of the dorso-median portion of this part and in some cases also parts of the dorsal spine; the extent of its area of drainage was influenced by the varying development of the other superficial veins in this part of the shield. The lateral inter-zonal vein emptied into the postero-lateral corner of the occipital vein sinus (pl. 56:3). In *C. signata* a ventral branch from the trunk entered the inter-zonal endoskeleton (pls. 31:4; 32:1, *vsocv)* and joined the lateral inter-zonal vein not far fram its entrance into the sinus. The median vein, the median inter-zonal (superficial) vein *(vizm,* pls. 11:4; 24:2; 36:2; 67:2; 100:3; 106—107), when developed, drained through its branches a dorso-median region of the shield, the most posterior part of the dorsal sensory field (cf. pl. 36:2, *vizms),* and an area behind this field; the vein entered the canal d_1, which also enclosed the ductus endolymphaticus, and emerged from this canal into the postero-median corner of the occipital vein sinus.

Veins from the anterior part of the neural canal which most probably were transformed vertebro-medullar veins emptied into the occipital vein sinus (vvm_1d, vvm_1s, pls. 13; 15:2) or into a longitudinal vein, in the canal *vct* which came from the antero-dorso-median parts of the trunk cavity and opened into the antero-ventral part of the occipital vein sinus (this vein possibly received tributaries both from the trunk cavity and from the outer region of the inter-zonal part; cf. fig. 11C; pls. 31:4; 32:1, vvm_1, vvm_2, *vvma, vvmb, vvmc, vct).* The occipital vein sinus also received a small vein from the vagus ganglion complex (fig. 11C; pl. 31:4-6, *v*).

It is of interest to observe that in *Petromyzon* veins from the most posterior parts of the brain and the anterior part of the medulla spinalis, probably remnants of vertebro-medullar veins, empty into the v. cerebralis posterior (Cori 1906, pp. 50—51; fig. 1; Hatta 1922, p. 183; pl. 22) and that this vein sometimes is sinus-like (cf. de Beer 1924, p. 326). The occipital vein sinus in the Osteostraci can be regarded as a widened part of the v. cerebralis posterior, and the different branches of the sinus as tributaries of this vein; as usual (cf. e. g. Gelderen 1924) the v. cerebralis posterior joined the v. capitis lateralis laterally to the vagus ganglion.

Vertebro-medullar veins which were transmitted in canals running from the neural canal and piercing the dorso-median part of the roof of the trunk cavity (*vvm*, vvm_2, vvm_3, pls. 13—14; 15:1; 16:2; 17; 39:3) possibly opened into the most anterior part of the v. cardinalis posterior. In some cases a vertebro-medullar vein emptied into one of the dorsal segmental veins which drained the dorsal spine (cf. *vvm, vsd,* fig. 13; pl. 56).

In some species dorsal segmental veins entered from beneath the postero-dorso-median portion of the inter-zonal endoskeleton and ascended in some cases into the dorsal spine; superficial branches of them drained the dorso-median region of the inter-zonal part at the basis of the dorsal spine (cf. pl. 29:1, vsd_{1-5}; pl. 56; fig. 13, vsd_{1-5}, *vsds).* These dorsal segmental veins most probably discharged into the posterior cardinal vein.

The v. jugularis inferior was a paired vessel; it arose from the lateral end of the v. rostralis and the antero-median end of the v. marginalis in the most anterior part of the oralo-branchial chamber (cf. pls. 29:2; 30:1, *vrs, vmarg),* and went backwards probably rather near the floor of the oralo-branchial chamber; it issued from this chamber through the lateral parts of the opening for the truncus arteriosus or the common opening for the truncus and the oesophagus (it seems rather improbable that it could have pierced the postbranchial wall through the small canal *"fy"*, Stensiö 1927, figs. 33—35; 39—40; pls. 9—10; 20; cf. pp. 185, 226; the canal *"fy"* corresponds to the canal v_X, pl. 27:1, this paper). Behind the postbranchial wall the v. jugularis inferior probably united with the v. marginalis, and the common trunk thus formed joined its fellow of the opposite side of the shield and then opened into the sinus venosus. The v. jugularis inferior probably received many tributaries from the buccal cavity and the gill-region, i. a. the bucco-pharyngeal veins which in *C. signata* were lodged in the grooves *vbp* in the anterior part of the roof of the oralo-branchial chamber (pls. 29:2; 30:1).

The v. rostralis, often widened so as to form a rostral vein sinus, was a transversal vein, either situated in a canal in the most rostral part of the visceral endoskeleton (the ventral rim) or partly lodged in a groove most anteriorly in the roof of the oralo-branchial chamber *(vr, vrs,* pls. 9:6; 29:2; 30:1; 61; 78:2-3; 87:2; 108—109). Superficial vein branches from the dorsal side of the rostral part of the head and from the ventral rim emptied into the rostral vein *(vrd,* pls. 6:2; 8:1; 9:6; 13—14; 16:2; 18:2; 20:2; 29:1; 34:1; 36:1; 37; 61; 64:1; 70:1). Laterally the v. rostralis passed over into the v. jugularis inferior.

The v. marginalis *(vmarg,* $vmarg_1$, *vsmarg,* figs. 16—17; pls. 9:6; 18:1; 27:1; 29:2; 30:1; 36:1; 37; 40:2; 81:1; 83; 85; 86:2; 93:1; 94; 97:3; 99:2; 106—109; 110:2) was anteriorly, in the buccal region of the oralo-branchial chamber, in communication with the v. jugularis inferior. In the anterior part of its course the vein was situated either in a canal in the ventral rim of the visceral endoskeleton or partly in such a canal and partly in a groove in the antero-ventro-lateral part of the roof of the oralo-branchial chamber. More posteriorly it went wholly enclosed in a canal near the lateral margin of the shield. It went backwards to the zonal part of the shield and was here, at the boundary between the cephalic shield proper and the shoulder-girdle, widened so as to form a marginal vein sinus; the vein issued from the cephalic shield through an opening in the postbranchial wall. Behind this wall the vein (the post-zonal part of the marginal vein) probably joined the v. jugularis inferior, as said before.

During its course the v. marginalis received numerous superficial tributaries from the dorsal side of the lateral parts of the shield (pls. 37; 60; 70:1, *vms*) which branches in some cases originated as far medially as in the region inside of the lateral sensory field, and, furthermore, tributaries from the lower side of the ventral rim. Farther backwards, on the shoulder-girdle, superficial branches which came from the dorsal and ventral sides of the shoulder-girdle proper emptied into the marginal vein sinus (pls. 29:2; 38:1; cf. 86:2, *vvs*). The superficial v. scapularis (in the canal *vsc*, figs. 16—17; pls. 8:2; 12:4-5; 13—14; 18:1; 23:1; 28:2; 30:2; 36—37; 39:3; 70:1) joined the post-zonal part of the v. marginalis.

Blood from the pectoral fin was carried to the marginal vein by one or two vv. brachiales (*vbr*, vbr_1, vbr_2, *v?*, figs. 16—19; pls. 18:1; 28:2; 30:2; 38:1; 40:3; 98:3); the largest (*vbr*, vbr_1) of these veins, the main v. brachialis, emptied into the zonal part, the other (vbr_2, *v?*) into the post-zonal part of the v. marginalis.

The lateral division of the shoulder-girdle, the cornu, both its superficial and deeper parts, was drained by direct or indirect tributaries of the marginal vein. Thus, in *C. vogti* (fig. 16; pls. 12:5; 18:1), the only species in which their canals are known in any detail, a v. cornualis medialis (*vcm*, cf. also pls. 28:2; 60; 71:2) which ran along the inner margin of the cornu emptied into the (main) v. brachialis; it received several small vein branches, i. a. from the upper part of the cornu (cf. also pls. 23:1; 28:2; 36:1; 37, *vcos*). A large v. cornualis lateralis (*vclat*, see also pl. 28:2) with numerous side-branches which drained the lateral, and mainly the antero-lateral, part of the cornu opened into the lateral side of the v. marginalis, anteriorly to its posterior, widened part.

During its course the v. marginalis received a series of transversal veins (vv. transversales ventrales) which came from the inner or ventral parts of the oralo-branchial chamber; possibly these transversal veins joined the v. jugularis inferior (as supposed by Stensiö 1927, pp. 184—185, 226) so that there was formed a series of connecting cross-veins between this vein and the v. marginalis. The canals (or some of the canals) for these veins (v_2—v_9, v_x) are exposed in pls. 26:2; 27; 29:2; 70:1; 81:2; 94:2; 97:3; 99:1. The ventral transversal veins passed outwards to the marginal vein, the anterior ones from the ventro-lateral parts of the branchial fossae (but dorso-medially to their external grooves), the posterior ones from the interval between two adjacent fossae; the posterior transversal veins were situated more ventrally (and superficially) than the anterior ones and opened into the ventral side of the median, post-zonal, division of the v. marginalis. The first three transversal veins emptied into the anterior parts of the v. marginalis, the fourth and fifth ones into the marginal vein sinus and the most posterior ones (in the canals v_6—v_9, v_X) into the post-zonal division of the v. marginalis. The ventral transversal veins probably arose from vv. nutritiae branchiales (cf. pl. 27:2; 29:2, *vnbr)* which ran near the roof of the ventro-lateral part of the branchial fossae, and from veins which went in the connective capsule round the thymus (or thymus-like organ; cf. pls. 27:2; 29:2; 30:1, th_1—th_3) in each branchial fossa.

Most of the veins in the cephalic shield of the Osteostraci have by Stensiö (1927) and in this paper been compared with or homologized with veins in the head of *Petromyzon* (or fishes). So are the v. captitis lateralis and the v. cerebralis posterior made homologous with the corresponding veins in this form (Stensiö 1927, pp. 53, 74, 230—231), a procedure which seems wholly justified.

The v. marginalis is considered by Stensiö (1927, pp. 185, 228, 368) to have been homologous with the v. superficialis longitudinalis dorsalis. Although the homologization seems plausible, some points are, however, to be added. In *Petromyzon* the dorsal superficial longitudinal vein is closely connected by transverse commissures with the anterior cardinal vein (and has possibly arisen from connecting loops between transverse outgrowths from the anterior cardinal vein, cf. Hatta 1922, pp. 200—201). According to Cori (1906, pp. 76—77) the (deep) peribranchial (lymphatic) sinus (cf. Hoyer 1938) in the adult *Petromyzon* which are in communication only with the anterior cardinal vein probably arose from the superficial vein system in the branchial region (of which the v. superficialis longitudinalis dorsalis forms a part). In an American Ammocoetes the superficial longitudinal vein which is the v. superficialis longitudinalis dorsalis is short and joins the anterior cardinal vein between the second and third branchial arches (Daniel 1934, p. 328). In the Osteostraci the v. marginalis had no connections with the anterior continuation of the anterior cardinal vein (v. capitis lateralis) but was connected (at least anteriorly) with the v. jugularis inferior.

Stensiö (1927, pp. 368—369) assumes that the dorso-lateral superficial veins in the Osteostraci were probably homologous with the dorsal transverse superficial veins between the dorsal superficial longitudial vein and the anterior cardinal vein in *Petromyzon,* and that they had lost their connections with the v. marginalis because of the development of the lateral sensory field. It seems, however, probable that this field had interfered in no way with the disposition and development of the superficial vessels (cf. p. 123; pl. 60), and the homologization seems to be open to some doubt.

On the other hand, the dorso-lateral superficial veins 1—3 are considered to be represented by the v. facialis and the v. veli dorsalis in *Petromyzon* (Stensiö 1927, p. 370). The v. veli dorsalis is, however, a deeply situated vein in the velum and can impossibly be a transformed dorso-lateral superficial vein. The v. facialis arises, according to Hatta (1922, p. 182) from a transverse connecting vessel between the v. capitis lateralis and the splanchnic v. mandibularis but this is contradicted by the description and figures by de Beer (1924, pp. 324—327); here the v. facilis is represented as the anterior continuation of a vein which must be the v. superficialis longitudinalis dorsalis. The morphological significance of many of the different veins in the head of *Petromyzon* still seems to be very obscure (besides the examples referred to above, see also the so-called v. jugularis inferior or v. superficialis longitudinalis ventralis and the so-called v. cardinalis anterior or v. jugularis profunda). On the whole it is very difficult or impossible to compare the individual veins in the Osteostraci with those in *Petromyzon* and every attempted homologization seems rather doubtful (with the exception of that of the v.capitis lateralis and v. cerebralis posterior).

The interpretation of the vascular canals given above rests in the main on the same basis as that of Stensiö (1927) and the principal features in this interpretation cannot, in my opinion, be subjected to any reasonable doubt. It can be said (cf. Stensiö 1927, p. 231) that the vascular canals or, more particularly, the arterial canals in the Osteostraci on the whole can be readily interpreted in view of our knowledge of the vascular system in *Petromyzon,* and this fact supports the idea that the vascular system in the Osteostraci, although in many respects aberrantly or more elaborately developed than in the modern Cyclostomes, nevertheless was built after the same general plan as in these animals.

The scale-covered trunk division.

In this chapter we are dealing with that part of the trunk which follows behind the cephalic shield. As is known, a posterior part of the cephalic shield is shown (Stensiö 1927) to consist of an anterior division of the trunk which has become incorporated into the cephalic shield and rigidly and without apparent boundaries coalescent with it; it forms here the shoulder-girdle or the zonal part and the interzonal part.

The scale-covered trunk division is on the whole well known in only a very small number of Cephalaspids, viz. in *Hemicyclaspis* and in a few *Cephalaspis* species (Stensiö 1932, pp. 54—71; 81—83; 102—103; 112; 115; 121—122), in *Aceraspis* and *Hirella* and partly in *Ateleaspis* (Heintz 1939, pp. 38—70, 82—86, 91—94). Among other Osteostraci it is partly known in *Thyestes* (Stensiö 1932, pp. 59, 69, 170) and very imperfectly in *Trematapis* (Rohon 1894, pp. 215—219; Robertson 1938a, pp. 283—285).

In the Cephalaspids the squamation of the trunk consists of the following different scales: a dorsal unpaired series of 1) the dorsal median scales (the scutes of the dorsal crest, the dorsal ridge scales or the median dorsal scales, the fulcral scales and spines of the dorsal fins), paired transverse rows of 2) dorso-lateral scales, 3) lateral scales (the dorso-lateral and lateral scales in each row sometimes form a unit, the lateral scales in *Aceraspis, Hirella* and *Ateleaspis),* 4) ventro-lateral scales and 5) ventral scales. Besides these scales there are also the different minute scales on the caudal part of the trunk, on the anterior (when developed) and the posterior dorsal fins and on the caudal fin as well as irregularly disposed minute scales on the ventral side of the trunk. (See Stensiö 1932, pp. 54—59; Heintz 1939, pp. 39—70, 83—85).

The scale-covered trunk division of the Spitsbergen Cephalaspids is very rarely preserved. Stensiö (1927, p. 274; pl. 36:4) describes a trunk fragment, associated with a cephalic shield (doubtfully referred to *Cephalaspis* [*Securiaspis*] *staxrudi).* In the material treated in this paper we have only one specimen, in which the scale-covered division is associated with the cephalic shield *(Cephalaspis pinnifera).* Furthermore there is a detached, rather large part of this division (ENS no. 615) and a small trunk fragment (in the Palaeontological Museum, Oslo), both being indeterminable as to genus and species. The squamation of these two latter specimens agrees in all essentials, as far as it is preserved, with that in *Hemicyclaspis* or, with regard to the ventro-lateral scales, in *Cephalaspis,* as described by Stensiö (1932, pp. 54—59); it can only be noted that in no. 615 there is preserved a dorsal crest as in *Hemicyclaspis* and *Cephalaspis pagei* but that no large posterior scute, as described in them, has been observed in this crest.

The trunk division or, more exactly, its squamation, of *C. pinnifera* will be described in some detail in so far as it differs from that in other Cephalaspids.

In *C. pinnifera* (pls. 42; 43:2) the transverse scale rows on the trunk each consist of a number of dorso-lateral scales *(dls),* one lateral scale *(ls),* and one ventro-lateral scale *(vs);* no ventral scales are preserved.

While the dorso-lateral scales in *Hemicyclaspis* and other *Cephalaspis* species consist of one scale in each transverse row (this scale is often secondarily fractured and thus seems to consist of several scales) they are in *C. pinnifera* in most places really subdivided into a number of independent scales of different shape and size, some being long and rectangular, others short and quadratic. They are connected with each other and with the lateral scales by simple sutures. The overlapping and overlapped areas in the dorso-lateral scales are much narrower than those in the lateral scales; each area is occupying only about one-tenth of the breadth of a dorso-lateral scale.

The lateral scales *(ls)* are built as in other *Cephalaspis* species and in *Hemicyclaspis.* In cross-section (fig. 22B) they are fairly thick in the middle third of their breadth, while the anterior and posterior thirds are rapidly decreasing in thickness towards the margins; in its posterior third the scale is somewhat thinner than in its anterior third. The overlapping area of a lateral scale is about as broad as the overlapped area, each occupying slightly less than one third of the breadth of the scale (as is seen in the anterior part of the scale-covered trunk division). The articulating faces between the lateral and the ventro-lateral scales in each transverse row could not be made out in detail but seem to be developed as described in *Hemicyclaspis* (Stensiö 1932, p. 58).

The ventro-lateral scales *(vs)* consist mainly of a dorsal portion covering the ventral part of the lateral side of the trunk; the ventral portion of the scales (at least in the anterior part of the trunk) is very indistinctly developed and the angle between these portions is obtuse and rounded. No ventro-lateral processes are thus developed and there is no distinct ventro-lateral ridge.

If we now turn to the unpaired scale series in *C. pinnifera,* we must first note, that Stensiö (1932, pp. 59, 67, 88; fig. 22) has briefly described in this same specimen what he considers to be a real anterior dorsal fin covered by scale-like plates, situated immediately behind the dorsal median ridge of the cephalic shield.

Most anteriorly on the trunk and intercalated between the upper ends of the transverse rows of dorso-lateral scales there are three very imperfectly preserved scales, and a fragment of a possible fourth scale; the foremost one is lying just behind the dorsal spine of the cephalic shield. The third of these scales (pl. 42:1, $sdcr_3$) is seen to be saddle-shaped or fulcrum-like, consisting of a pair of ventro-lateral legs and a narrow, connecting, unpaired part. This scale evidently corresponds to an anterior dorsal scute of the dorsal crest in *Hemicyclaspis* or some *Cephalaspis* species (Stensiö 1932, pp. 54, 59) and to a median dorsal scale in *Aceraspis* and *Hirella* (Heintz 1939, pp. 39—41, 57—58, 85). The two anterior are very imperfectly preserved and present only in their ventro-lateral parts but it is beyond doubt that they are serially homologous with the third scale and that they all formed a series of unpaired dorsal scutes belonging to the dorsal crest. From what is preserved of the third scute it seems very probable that it cannot have been very high but was of approximately the same shape as the corresponding one in *Hemicyclaspis.*

Behind these scutes follows the structure which has been called the "dorsal fin". Before describing it we must point out that it is very

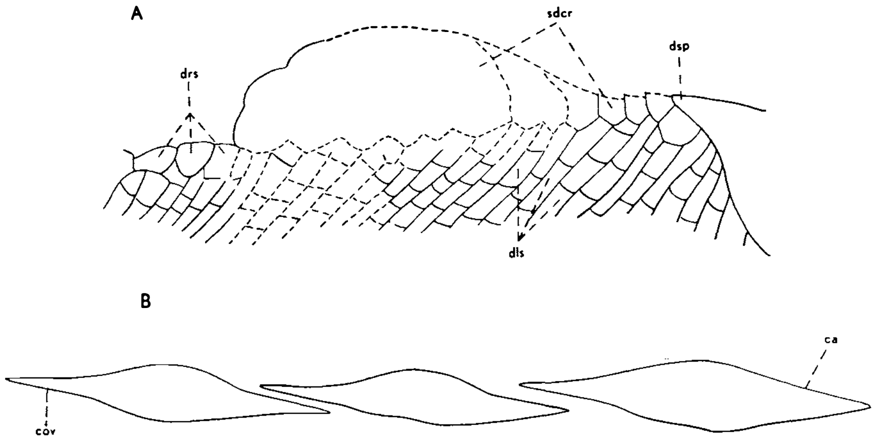

Fig. 22. — *Cephalaspis pinnifera.* A, partly hypothetical restoration of the dorsal crest; nat. size; B, semi-diagrammatical cross-section through three subsequent rows of lateral trunk scales; × 10.

ca, area overlapped by the scale in front; *cov,* overlapping area, partly covering the following scale; *dls,* dorso-lateral scales; *drs,* dorsal ridge scales; *dsp,* dorsal spine of the cephalic shield; *sdcr,* scutes of the dorsal crest.

imperfectly preserved, and the anterior half is for the most part present as an impression of its left side. It is therefore very difficult or impossible correctly to decipher the remains, and the following interpretation is thus only provisional.

At first view the "dorsal fin" (pl. 42:1, *d*) seems to be covered with many scale-like plates of different sizes. On closer examination (pl. 42:2), however, the "plates" are seen to be more or less continuous with each other so that the "dorsal fin" actually consists of one large undivided plate or scute, provided with long or short superficial grooves or with grooves or canals in its deeper parts. Possibly the anterior part of the plate is detached from the posterior part and constitutes a separate scute; the conditions are, however, very obscure in this part and cannot be fully clarified. The "fin" thus ressembles the posterior part of the anterior dorsal fin in *Aceraspis (*Heintz 1939, p. 59; figs. 19—20) or possibly more closely the first dorsal "fin" in *Ateleaspis* (Heintz 1929, fig. 34). In the posterior half of the plate the dorsal and postero-dorsal parts are distinctly thicker than the antero-ventral parts, consisting of reticular bone-tissue. The dorsal and postero-dorsal margins of the plate are not sharp-edged but broad and rounded. Viewed sideway the posterior margin of the plate is convex. No traces of any fin membrane are present. The basal parts of the plate are very imperfectly preserved and are present only on the left side; the ventrolateral margin of the plate is provided with several projecting angles which are connected by sutures to the uppermost ends of the dorso-lateral scales. It seems very probable that the plate was somewhat saddle-shaped with a shallow basal cavity, and thus the plate would resemble the ventro-lateral scales of e. g. *Cephalaspis pagei* (Stensiö 1932, fig. 18; cf. p. 69) much more than the normal scutes of the dorsal crest in *Hemicyclaspis* or other *Cephalaspis* species.

The whole plate can be interpreted as being formed by the fusion of separate fulcum-like scales like those in *Aceraspis* and *Hirella*. It can be compared in this respect with the posterior dorsal scute in *Hemicyclaspis* and *Cephalaspis pagei* (Stensiö 1932, pp. 54, 59, 68; pls. 2:2, 4; 3:4; 35:3) and in *Ateleaspis* (Heintz 1939, p. 93; fig. 34), and with the fin scute in *Tremataspis* (Robertson 1938a, p. 284; pls. 1:1; 3:3-4; cf. Patten 1912, fig. 241).

We thus find that in all probability the so-called dorsal fin in *C. pinnifera* is on the whole similar to that in other Cephalaspids and that it does not form any real fin but consists of a dorsal crest which is unusually high in its middle and posterior parts.

The anterior division of the dorsal fin-fold (cf. Stensiö 1932, pp. 68—69) behind the cephalic shield is here interpreted as being covered in its most ventro-lateral parts by the uppermost dorso-lateral trunk scales and for the rest by a series of unpaired scutes, and, more precisely, by three normally developed fulcrum-like dorso-median scales or dorsal scutes, lying immediately behind the dorsal spine of the cephalic shield, and possibly one or two scutes which form the transition between the anterior scutes and the posterior one, which is a very long and rather high dorsal scute. The (in many ways) hypothetical shape of the dorsal crest is shown in the restoration in fig. 22A.

If I am right in this interpretation of the rather obcure, actual remains, the difference between the conditions in *C. pinnifera* and those in *Hemicyclaspis, Ateleaspis,* and other *Cephalaspis* species, known in this respect, is rather insignificant (cf., however, *C. patteni,* p. 246).

Heintz (1939, p. 60) has shown that the anterior dorsal fin in *Aceraspis* (and *Hirella*) is built after the same plan as the dorsal crest in other Cephalaspids; there is thus only a difference in degree between what is called an anterior dorsal fin and a dorsal crest in the Cephalaspids.

Behind the dorsal crest there are preserved three dorsal ridge scales (pl. 42:1, *drs*) of normal shape.

Posteriorly to these scales and above the most posterior rows of lateral scales the dorsal portion of the trunk is covered with rather small irregularly disposed scales instead of regular rows of dorso-lateral scales. In comparison with the similar conditions in *Hemicyclaspis* (Stensiö 1932, p. 56) we can assume that this irregular disposition of the scales was due to the influence of a posterior dorsal fin situated dorsally to them. Nothing is, however, preserved of such a fin.

Also the small proximal part of the caudal region of the trunk, which is present in the specimen, is covered with rather small irregularly disposed scales (pl. 42:1, *cs*).

Mode of living.

The head of the Cephalaspids was always depressed and more or less expanded in lateral direction, especially by the development of flattened cornua. The hypobranchial part of the head was horizontal; the mouth was subterminal or ventral and the branchial openings situated on the ventral side.

By reason of the weight of the cephalic shield, the enclosure of the posterior part of the trunk in a sheat of dermal plates and the generally depressed form of the body the Cephalaspids were probably rather heavy-bodied, little active and sluggish swimmers. As has been pointed out by Stensiö (1927, p. 19) they must have been benthonic forms.

It is known (cf. Stensiö 1932; Heintz 1939) that the tail in *Hemicyclaspis* and allies and in *Cephalaspis* is heterocercal, and it can be noticed that these forms also had well developed pectoral fins. The shape of the tail is unknown in such forms as e. g. *Tremataspis,* in which the pectoral fins are lacking, but from what is known of the caudal part of the trunk (Rohon 1894; Robertson 1938a) it seems not unlikely that the caudal fin was diphycercal, and this or the hypocercal form would, as pointed out by Robertson (1938a, p. 184; cf. pp. 185, 285), seem to be the most likely one from a functional point of view.

The significance of the heterocercal (epibatic) fin has been frequently discussed with regard to modern fishes but it seems not yet to have been fully understood, as the action of the caudal fin in the swimming fish is moderated by many other factors in the shape of the body and the position of the paired fins. The most common view is that the action of a heterocercal fin, while propelling the fish forwards, drives the front end of the fish (that part of the body lying anteriorly to the centre of gravity) downwards while the tail of the fish is turned upwards (Schulze 1893; Ahlborn 1895; Breder 1926, p. 225; Rauther 1933, p. 513). Experimental studies with models (Grove & Newell 1936; Harris 1936) have shown that the action of the heterocercal fin, while being propulsive, really results in a raising of the rear part of the fish. According to Schmalhausen (1916, pp. 211—212) the heterocercal fin in connection with a trihedral trunk acts in such a way that it drives the fish straight forwards (cf. Rauther 1933, p. 514).

In the Cephalaspids the resultant of the action of the heterocercal caudal fin and the weight of the cephalic shield would have turned the anterior part of the body downwards and this movement would perhaps in some measure have been counteracted by the generally trihedral form of the head and trunk and been regulated by adjustments of the pectoral fins. The cornua probably acted as gliding-planes ("hydrofoils", Westoll 1945, p. 350) or balancers and contributed to the stability of the animal. In case of reduction or absence of the cornua, as e. g. in *Axinaspis,* the pectoral fins possibly partly took over their function in having aquired the possibility to move in lateral direction by means of certain abductor muscles. Possibly the Cephalaspids also could rest on the sea-bottom, supporting themselves on the pectoral fins as do the Cottids among recent Teleosts. This action would imply that the pectoral fins were rather movable in ventral direction and the presence of this function can possibly be deduced from the shape of the pectoral sinus in certain forms (cf. p. 35 and Zych 1937, p. 65).

The Cephalaspids were certainly microphagous, much as the Ammocoetes larvae of recent Petromyzonts (cf. Stensiö 1927, pp. 19—20).

Systematic description.

Family Cephalaspididae.[1]

1927. Cephalaspidae, Stensiö.
1932. Cephalaspidae in part: Cephalaspinae + Kiaeraspinae in part, Stensiö.
1935. Cephalaspidae in part: Cephalaspinae + Kiaeraspinae in part, Robertson.
1939. Cephalaspidae (Cephalaspinae + Hemicyclaspinae) + Kiaeraspidae (in part?), Heintz.
1940. ? Cephalaspidae, Berg.
1945. Cephalaspidae in part: Cephalaspinae + Hemicyclaspinae + Kiaeraspinae in part, Robertson.
1951. Cephalaspidae in part + Ateleaspidae in part + Kiaeraspidae, Denison (1951a). (Older synonyms omitted.)

Diagnosis. — Osteostraci with cephalic shield well developed and extending more os less backwards on trunk. Cornua well developed or replaced by lateral angles on shield or entirely absent. Sensory fields consisting of one unpaired dorsal field and one, two, three or four pairs of lateral fields. Five nerve canals on each side running from labyrinth cavity to lateral field or fields: first nerve canal sigmoidally bent, proximal part lying closely to orbit; distal part undivided or divided into two strong main branches. Canal for r. mandibularis passing down to oralo-branchial chamber between branches of first nerve canal to lateral sensory field or between this canal and second canal to lateral field, very seldom just in front of first nerve canal. Canal for dorso-lateral superficial vein 3 opening into orbit or into canal for v. capitis lateralis closely behind orbit. Canal for postorbital division of v. capitis lateralis running from posterior part of orbit in (almost) straight posterior direction. Infraorbital sensory line running from lateral side of orbital opening in antero-lateral direction over to lateral (visceral) part of shield, generally traversing lateral sensory field, meeting its fellow of other side of shield between antero-lateral ends of lateral fields. Oralo-branchial fenestra with rather small plates. Pectoral fins present. Scale-covered anterior dorsal fin present or represented by dorsal crest, covered with unpaired series of scutes. Posterior dorsal fin present. Squamation on trunk formed by dorsal unpaired ridge-scales, transverse rows of lateral (or dorso-lateral and

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[1] This is the correct and only permissible form of the name (cf. Int. rules of zool. Nomenclature, Art. 4).

lateral) and ventro-lateral scales, and by ventral and caudal scales. Exoskeleton composed of three different layers; basal layer without basal cavities (except in sensory fields); middle layer usually with radiating vascular canals.

Remarks. — The diagnosis given above is only preliminary and includes many characteristics observed only in a few forms.

The family as here defined corresponds only to a part of the family "Cephalaspidae" as conceived by Stensiö (1932, p. 74); it includes his subfamily "Cephalaspinae" and of his subfamily "Kiaeraspinae" the first group of genera, viz. *Benneviaspis, Securiaspis, Hoelaspis, Boreaspis* and *Kiaeraspis.* The genera of the second group in this subfamily *(Thyestes, Didymaspis, Sclerodus)* are here considered as not belonging to the family. Heintz (1939) follows Stensiö in the major subdivisions of the Osteostraci, the only obvious differences being that he erects the new subfamilies "Hemicyclaspinae" and "Cephalaspinae", and in doing this he also raises the former subfamilies of Stensiö to the rank of families and the families to suborders. The system of Robertson (1945) does not diverge on principle from that of Heintz and Stensiö, his "Kiaeraspinae" is of the same extent as in Stensiö's paper, only the genus *Didymaspis* is placed in a family of its own (and two new genera, *Witaaspis* and *Saaremaaspis)* are added to the subfamily). With regard to Berg's systematic survey it seems not clear if the family "Cephalaspidae" includes the subfamily "Kiaeraspinae" of Stensiö or if this subfamily is placed in the family Thyestidae. In Denison's (1951a) arrangement *Hemicyclaspis* and allied genera, as well as *Witaaspis,* are placed in a family of their own, "Ateleaspidae", *Thyestes* (and *"Procephalaspis")* is included in "Cephalaspidae", and *Kiaeraspis* is placed in a family of its own.

As my concept of the family differs from that of previous authors, and as the boundary between the family Cephalaspididae as defined in this paper and the other Osteostraci cuts through one of the former subfamilies leaving only a part of it within the family, it seems appropriate here to discuss some of the features used by Stensiö (1932, pp. 75, 76, 151) in separating the two subfamilies "Cephalaspinae" and "Kiaeraspinae". As an important characteristic the disposition of the first nerve canal to the lateral sensory field *(sel_1)* must be considered. In "Cephalaspinae" this canal runs undivided from the labyrinth cavity only as far as to a point just antero-laterally or laterally to the orbit, the independent branches of the canal being thus fairly long. In "Kiaeraspinae" the canal remains undivided for a greater distance or to a point about midway between the orbit and the lateral field, or else the canal runs undivided even as far as to the median margin of this field. It is evident that we have here to do with a, in reality rather vague, difference in degree. To this can be added that the character varies considerably, as in *Securiaspis kitcheni* (Stensiö 1932, pl. 49:1), *Benneviaspis* (cf. Stensiö 1932, pls. 47:1; 48:1), *Hirella gracilis* (Heintz 1939, fig. 27; this fact has already been noted by Westoll 1945, p. 351) and *Boreaspis robusta* (p. 479; pl. 78:1, 3); also within the genus *Cephalaspis* irregularities occur, as in *Cephalaspis* sp. (Stensiö 1932, pl. 21:1), *C. dissimulata* (p. 291; pls. 1:2; 8:1), and *C. eurhynchus* (p. 265; pls. 4; 5:5); in *C. excellens* and *C. vogti* the first nerve canal is virtually undivided (pls. 12:5; 13; 16:2; cf. Stensiö 1927, pl. 27). It thus seems clear that the presence or absence of the branches of the canal sel_1 or, in the former case, their different length, cannot be a systematic character of primary importance. It is, however, used in the following in the definitions of the genera within the subfamily.

A second point in the diagnoses of the two subfamilies says that the r. mandibularis trigemini (in the canal V_3) passes down to the oralo-branchial chamber either entirely behind the nerve canal sel_1 and its branches or in the space between the branches or, finally, entirely in front of this canal. The first alternative distinguishes the subfamily "Kiaeraspinae" and more precisely the first group of genera in this subfamily, viz. *Benneviaspis, Securiaspis, Hoelaspis, Boreaspis* and *Kiaeraspis* (here called the *Kiaeraspis* group); the second alternative is characteristic of the subfamily "Cephalaspinae" and the third one of the subfamily "Kiaeraspinae", the second group of genera with *Thyestes, Didymaspis* and *Sclerodus* (here called the *Thyestes* group).

In the first place and with regard to the *Kiaeraspis* group we can now observe that the canal V_3 in *Kiaeraspis* and *Boreaspis* opens into the oralo-branchial chamber behind the canal sel_1 (pls. 78:3; 82:1; 85; 86:2; 89:2; 91:2; 93; 94:2; 97:1; cf. Stensiö 1927, pls. 14; 49), in *Hoelaspis* very far laterally and ventrally to the posterior branch of the canal sel_1 (Stensiö 1927, pl. 45), in *Benneviaspis* under the posterior branch of the canal sel_1 or possibly in front of this branch (pls. 70:1; 71:2) and that in *Securiaspis* the posterior branch of the canal V_3 is disposed as in *Benneviaspis* while the anterior branch of the canal V_3 opens into the oralo-branchial chamber between the two branches of the canal sel_1 (pl. 62:1); when the canal sel_1 is deeply forked (as on the left side in *S. kitcheni,* see Stensiö 1932, pl. 49:1) the canal V_3 is disposed exactly as in a normal *Cephalaspis* species, that is, it opens downwards in the space between the branches. In this connection it must, however, be noted that in the new species *Cephalaspis excellens* (p. 314) the canal V_3 enters the oralo-branchial chamber far medially and immediately in front of the canal sel_1. In the new genus *Acrotomaspis,* probably related to *Kiaeraspis,* the canal V_3 in its proximal course through the visceral endoskeleton runs closely behind the canal sel_1 but crosses the distal part of this canal on the ventral side and opens into the oralo-branchial chamber just antero-laterally to this canal (pl. 103:1, 4). From all this it is evident that the disposition of the canal V_3 in relation to the canal sel_1 or its branches in the *Kiaeraspis* group and in *Cephalaspis* depends mostly upon the more or less deep bifurcation of the canal sel_1. As we regard this latter character as of a minor systematic value it follows that this applies also to the disposition of the canal V_3 in *Cephalaspis,* as opposed to the conditions in the *Kiaeraspis* group.

In the *Thyestes* group, however, the matter is different. In this group the canal sel_1 is placed so far backwards that the canal V_3 runs considerably in front of it, and the canal for the n. facialis *(VII)* is said to behave in the same way too (cf. p. 551). We find also another fact of importance, not sufficiently observed previously, i. e. the different proximal course of the canal sel_1: in *Cephalaspis* and in the *Kiaeraspis* group the canal sel_1, after leaving the labyrinth cavity, goes to the posterior or postero-lateral wall of the orbit and then lies closely to the orbit, along its postero-lateral and lateral walls, and first at the antero-lateral corner of the orbit it turns in antero-lateral direction towards the lateral sensory field; the canal sel_1 is thus in its proximal course sigmoidally bent. In the *Thyestes* group, however, the canal sel_1 lies rather far posteriorly to the orbit and runs in almost straight direction towards the lateral sensory field. All these differences with regard to the canal sel_1 and its relation to the canal V_3 (and *VII?)* I regard as taxonomically rather important, and with the application of this character we cannot separate the subfamilies "Cephalaspinae" and "Kiaeraspinae" of Stensiö but most draw the dividing-line between on one side the subfamily "Cephalaspinae" together with the *Kiaeraspis* group in the "Kiaeraspinae" and on the other side the *Thyestes* group in the "Kiaeraspinae".

The difference between the two groups in the "Kiaeraspinae" with regard to the relation of the canals sel_1 and V_3 is also noted and emphasized by Westoll (1945, p. 351).

With regard to the last character used by Stensiö in the diagnoses of the two subfamilies, the opening of the canal for the third dorsolateral superficial vein into the orbit or into the canal for the postorbital division of the v. capitis lateralis, it is indirectly said (Stensiö 1932, pp. 76, 156) that exceptions occur. As seen e. g. in *Securiaspis* (pls. 62:1; 63:2; 64:2; Stensiö 1932, pl. 49:1) and in *Thyestes* (Stensiö 1932, pls. 50:3; 51:2) it is not even a stable generic character. It can accordingly not be used with great confidence for the separation of subfamilies or families.

Summing up, we must consider the subfamily "Cephalaspinae" and the *Kiaeraspis* group (of the subfamily "Kiaeraspinae") to form a distinct aggregation of allied genera and as these genera most probably are more closely related to each other than to any of the genera of the *Thyestes* group they are separated from this group and placed in a distinct family, Cephalaspididae.

Westoll (1945, p. 352) has noted the unsatisfactory in the characters normally used in classifying the Osteostraci, and, after discussing some of the characters, he proposes to distinguish certain assemblages of probably genetically related genera, and as such assemblages he mentions the "Hemicyclaspinae", the "Kiaeraspinae" s.s. (= the *Kiaeraspis* group) and the *Thyestes* group.

Besides the characteristics of the family Cephalaspididae mentioned in the remarks above there are also some others used in the diagnosis, which will be discussed later in the remarks upon the other Osteostraci (p. 550). Here it will only be noted that the characters taken from the structure of the trunk and fins are known only in a very few forms and that very little is known of their variation and systematic value; they are, however, provisionally included in the diagnosis.

A rather remarkable fact in the morphology of the family is the variable development of the lateral sensory fields. In most of the genera they are normally developed, that is, there is only a single field on each side of the shield. The genus *Axinaspis* is, however, distinguished in having the single field replaced by two small fields. In *Nectaspis* there are three fields, and in *Acrotomaspis* no less than four fields are found on each side of the shield. In *Boreaspis* some species have a single field while in others the field is subdivided into two fields by a rather small intervening space. In a specimen of *B. curtirostris* the lateral field, which in most specimens of the species is undivided and of uniform breadth is by a narrow interval divided into two portions (pl. 92:3). A similar condition is seen in one specimen of *Kiaeraspis auchenaspidoides* (pl. 97:2). In all these aberrant forms the nerve canals for the lateral fields, as far as known, are disposed in quite the same manner as in other normal forms. It is thus evident that merely the presence of two or more lateral sensory fields instead of one on each side of the shield is a character of minor systematic importance unless it is accompanied by a re-disposition of the supplying nerve canals.

The backward extent of the exoskeletal component of the interzonal part of the cephalic shield is subject to some variation. In *Cephalaspis, Ectinaspis* and *Tegaspis* it reaches backwards to some distance behind the endoskeleton (cf. Stensiö 1927, fig. 7; 1932, fig 3). In *Kiaeraspis* (Stensiö 1927, fig. 8), *Axinaspis* and *Acrotomaspis* the exoskeleton is greatly developed and forms a major portion of the interzonal part which in these genera is extended far backwards on the trunk. *Nectaspis* and *Securiaspis* occupy in this respect an intermediate position between *Cephalaspis* and *Axinaspis.* In *Benneviaspis, Hoelaspis* and *Boreaspis* the exoskeleton does not extend or extends very little behind the endoskeleton and has thus posteriorly the same or almost the same boundary as the underlying endoskeleton. The posterior margin of the inter-zonal part between the posterior and the postero-lateral angles is distinctly indented so as to form an inter-zonal sinus.

As is seen from the following systematic account the family Cephalaspididae includes many forms, differing widely in their habitus but forming a rather homogenous group with regard to the internal structures of their shields. At present it does not seem necessary or advisable to divide the family into subdivisions of lower order more than the two subfamilies Ateleaspidinae and Cephalaspidinae (after Heintz 1939). Within the subfamily Cephalaspidinae we can, however, place some of the genera in separate groups, each including genera supposed to be genetically related, and representing distinct evolutionary lines within the family. Besides the characters mentioned below there very probably are other anatomical structures which will distinguish the different groups.

One such group of genera is formed by *Benneviaspis, Hoelaspis* and *Boreaspis,* and is characterized by the exoskeleton not extending much behind the endoskeleton on the inter-zonal part of the shield, which has distinct and often deep inter-zonal sinus, by the lateral sensory fields extending with a postero-median process on to the zonal part in front of the pectoral sinus or even farther backwards on to the inter-zonal part, by the first nerve canal for the lateral sensory field being undivided or divided into two branches only to about midway between the field and the orbit, by the absence of a dorsal median ridge on the inter-zonal part, and by a similar structure of the exoskeleton and the development of the mucous canal system. The genera *Hoelaspis* and *Boreaspis* are in fact very similar and the former may be considered a possible ancestor to the latter.

Ectinaspis approaches this group in some respects (see p. 443). *Tegaspis* shows a similar disposition of the first nerve canal of the lateral sensory field as in the genera just mentioned, and a similar shape of the lateral sensory field as in *Boreaspis;* in other respects, however, the genus is quite dissimilar and has probably no very close affinity either to the genera *Benneviaspis, Hoelaspis* and *Boreaspis* or to *Ectinaspis. Tegaspis* would possibly, through the species *Cephalaspis? pedata,* seem to be related to *Cephalaspis.*

A second group within the subfamily is formed by the genera *Kiaeraspis, Axinaspis* and *Acrotomaspis,* representing another line of evolution; the group is distinguished by the very slight or even non-development of the cornua and by the great extent backwards of the inter-zonal part, the exoskeleton of which is closed ventrally, by the undivided first nerve canal for the lateral sensory fields, and by the subdivision or tendency toward subdivision of the lateral sensory fields.

The genus *Nectaspis* may possibly in some way be genetically related to these last mentioned genera, but differs from them in some important features: the inter-zonal part is not extended very much backwards on the trunk and is furthermore not closed ventrally, on the other hand the preorbital part of the shield is rather strongly developed and a high velar ridge is present. The subdivision of the lateral fields has in this genus gone rather far, and the lateral field on each side of the shield is constantly replaced by three small fields.

The genus *Securiaspis* is apparently not closely related to any of the afore-mentioned genera and appears to be most nearly allied to *Cephalaspis* but it is not possible now to point out the particular species group in this genus to which it would be genetically connected. The genera *Cephalaspis* and *Securiaspis* may thus form a third group but it must be emphasized that the genus *Cephalaspis* may possibly turn out to be a heterogeneous assemblage including disparate elements, thus representing several evolutionary lines.

Subfamily Cephalaspidinae.

Diagnosis. — A subfamily of Cephalaspididae with cephalic shield provided with cornua, these sometimes represented by lateral angles on shield. Pectoral sinus usually present. Pectoral fins well separated from cephalic shield and from trunk. Inter-zonal part of shield long or short, its exoskeleton generally closed ventrally. Lateral sensory field on each side of shield single or subdivided, posterior part of field or posterior field reaching far backwards, ending on cornua or on inter-zonal part.

Genera: *Cephalaspis* Agassiz, 1835, *Benneviaspis* Stensiö, 1927, *Hoelaspis* Stensiö, 1927, *Boreaspis* Stensiö, 1927, *Kiaeraspis* Stensiö, 1927, *Securiaspis* Stensiö, 1932, *Ectinaspis* n. g., *Tegaspis* n. g., *Axinaspis* n. g., *Acrotomaspis* n. g., *Nectaspis* n. g.

Genus **Cephalaspis** Agassiz.

1835. *Cephalaspis* in part, Agassiz, p. 135.
1870a. *Cephalaspis* in part (subgenera *Eucephalaspis* + *Zenaspis)*, Lankester, p. 43.
1891. *Cephalaspis* in part, Woodward, p. 177.
1927. *Cephalaspis* in part, Stensiö, p. 246.
1932. *Cephalaspis,* Stensiö, p. 87.

Diagnosis. — A cephalaspid genus with cephalic shield more or less triangular in outline, rostral part rounded, angular, or protracted into a short rostral process. Cornua well developed, projecting in posterior or postero-lateral direction, generally extending backwards behind level of posterior angle of inter-zonal part. Pectoral sinus generally well defined. Inter-zonal part generally short. Sensory fields well developed, consisting of one dorsal, and two lateral fields; lateral fields extending backwards at least to basal part of cornua, without any distinct postero-medial corner or process on to zonal part in front of pectoral sinus. Orbital openings generally situated before middle of length of cephalic shield in median line. Common naso-hypophyseal opening or separate nasal and hypophyseal openings. First nerve canal for lateral sensory field generally divided into two branches just antero-laterally to orbit, exceptionally running undivided to lateral field. Canal of dorso-lateral superficial vein 3 generally opening into postero-dorso-medial corner of orbit. Middle layer of exoskeleton with radiating vascular canals.

Type species. — *Cephalaspis lyelli* Agassiz (Woodward 1891, p. 179).

Remarks. — The diagnosis given above closely follows in part that of Stensiö in his monograph of the Cephalaspids of Great Britain (1932, p. 87) but is altered in some respects owing to the inclusion in the genus of some aberrant species. Some of these points will be considered below.

In most of the species the first nerve canal for the lateral sensory field (sel_1) divides just antero-laterally to the orbital openings into two strong branches, and this disposition is thus the normal one for the genus. In the species *C. excellens* and *C. vogti,* however, the canal runs undivided as far as to a point just medially to the lateral field and here divides into small diverging branches in the same manner as do the other nerve canals for the lateral field. The disposition of the canal is thus seemingly the same as in e. g. *Boreaspis, Hoelaspis,* and *Kiaeraspis* and this condition would be thought to indicate a nearer kinship of *C. excellens* and *C. vogti* to these genera than to *Cephalaspis* and thus also to justify their placing in a separate genus. We must, however, observe that the canal sel_1 mainly lies behind the canal V_3 in the two species in question whereas in *Boreaspis* and others the canal sel_1 in the main part of its course lies in front of the canal V_3. The case is, furthermore, complicated by the conditions in some other species, which seem to deprecate a taxonomical procedure just suggested. In one specimen of *C. dissimulata* the canal sel_1 is undivided just as in *C. excellens* and *C. vogti* but in another specimen of the same species the canal is divided into a rather wide anterior and a posterior somewhat narrower branch (pl. 1:2). Furthermore in a *Cephalaspis* species from Great Britain, figured by Stensiö (1932, pl. 26:1), the canal sel_1 (“sel_1”, “sel_2”) on the left side is divided into two branches, although the branching takes place somewhat more antero-laterally than in most of the *Cephalaspis* species; on the right side of the same shield, however, the corresponding canal (“sel_2”) runs undivided as far as to the lateral field. All this seems to indicate that the development of the first nerve canal for the lateral sensory field is not always a stable character in the genus, and that it can vary not only in the same species but also within the same specimen. The fact that anomalies may occur in the development of the nerve canals for the sensory fields is furthermore proved by the conditions in a specimen of *Boreaspis macrorhynchus,* where on the left side of the cephalic shield there are six nerve canals as against the normal number of five (see p. 493 and pl. 95:2). In *C. excellens* there is also another aberrant feature, i. e. the presence of separate openings for the nasal and the hypophyseal ducts; this character, however, also occurs in *C. eurynotus* and *C. dissimulata* (in some specimens), in other respects quite typical *Cephalaspis* species, and thus seems to be of slight importance in systematic respect. It is impossible to draw a distinct dividing line between on one side a supposed segregation, including *C. excellens* and *C. vogti,* and on the other side the genus *Cephalaspis,* and as the two species in other respects are quite *Cephalaspis*-like, they are here included in the genus *Cephalaspis.* In this connection it can be noted that the canal sel_1 in *Cephalaspis,* as a rule, is either divided centrally to near the orbit or else is altogether undivided; intermediate stages are seldom met with (see *C. eurhynchus,* p. 265). The presence of an undivided canal sel_1 in the species mentioned can be explained as an abortion of the rudiment of one of the branches of the canal during the ontogenetic development, which in some species *(C. dissimulata)* occurs only occasionally but in others *(C. excellens, C. vogti)* has become the rule. If this be true, the presence of an undivided canal is in these cases a secondary character of no great phylogenetic and systematic importance. However, the conditions in these two later species can possibly be a vestige of a more primitive stage such as exhibited in e. g. *Thyestes.*

In the definition of the genus given above attention is paid only to the characteristics of the cephalic shield in order to make it uniform with those of the other genera, in which the scale-covered trunk is unknown. Stensiö (1932, pp. 87—88) has included in his definition also several features taken from the scale-covered trunk division and the fins: "Trunk generally triangular in cross-section. Pectoral fins well developed. Anterior dorsal fin represented only by long dorsal crest, consisting of an unpaired series of large scutes. Posterior dorsal fin situated far backwards with strong anterior spine composed of fulcral scales. Caudal fin heterocercal but with vestiges of ventral axis supporting a partly independent lobe. Squamation consisting of unpaired scutes of dorsal crest and unpaired ridge-scales dorsally, and under these in each transverse row, one or more dorso-lateral scales, one lateral scale, one ventro-lateral scale (in front perhaps two or three) and several ventral scales. Ventro-lateral scales of each row extending medially to cover lateral part of ventral surface of trunk." The sentence about the caudal fin must, however, (after Heintz 1939, pp. 65—68;

fig. 25) be altered to: Caudal fin heterocercal, in antero-ventral part with horizontal membrane.

The classification of the family is at present necessarily built upon differences in the structure of the cephalic shields.

Cephalaspis is here, as by Stensiö (1932, p. 88), regarded as a provisional genus, and for the reception in it of most of the species referred to it, we only include in the diagnosis characters taken from the cephalic shield.

The "*Cephalaspis*-like species from Spitsbergen" (*C. pinnifera* in this paper), which according to Stensiö (1932, p. 88) must be excluded from the genus and placed in a new genus, is a true *Cephalaspis,* even if the genus is taken in a restricted sense, since the so-called dorsal fin is built essentially like a dorsal crest.

In this connection we can remark that the conditions in *C. patteni* seem to be somewhat aberrant with regard to the dorsal fins. The remains are, however, rather obscure, and it is difficult to get a clear picture of the structures. From the restoration given by Patten (1912, fig. 234) and the description of the same specimen by Robertson (1936, pp. 291—292) it seems established that there is a very long dorsal fin, evidently covered by lepidotrichia-like scales and very probably, at least in part, representing the posterior dorsal fin in the other species; nothing is known whether there was a small separate anterior dorsal fin or dorsal crest or not, nor if the anterior and posterior dorsal fins formed a single continuous fin.

The majority of the *Cephalaspis* species are, as said above, known only from their cephalic shields. Many species included in the genus, are furthermore unknown as to the inner structure of the shield, and these species are thus, because of their resemblance to better known species, placed more or less provisionally in the genus.

The definition and determination of the *Cephalaspis* species was rather difficult already before now (Stensiö 1932, p. 89), and with the increase of the number of species, which is the result of the working up of the new collections from Spitsbergen, this is rendered much more difficult still. In many cases the specimens can be specifically determined only after a thorough consideration of a large number of characters and a careful comparison with other specimens. The cephalic shields must thus be rather completely and well preserved, and when this is not the case the specimens must often be left undetermined.

A number of characters used for distinguishing the different species is given by Stensiö (1927, p. 246; 1932, p. 88), and these characters together with a few others are used also in the present paper. The characters or group of characters are considered below with short remarks on their applicability and their variation (the characters relating to the structure of the trunk and fins are omitted as they are not applicable to the Spitsbergen material, in which the species in almost all cases are known by their cephalic shields only).

The size of the species (as indicated by the size of the cephalic shield): there seems to be very little variation in the size of the shield in each species (as is noted before, p. 52), the shields preserved are always from fullgrown individuals, those of the juvenile ones were not ossified and have thus not been fossilized); the variation on the length of the shield in a single species seems to be at most about 20 % of the mean length. The general shape and proportions of the shield: this is generally expressed in the diagnoses only by stating the relation of the maximum breadth to the length in the median line; these statements must not be taken too literally in such cases where the material of the species is limited and the variation is unknown. In several instances (see e.g. *C. excellens, C. hyperboreus)* is has namely been found that the variation is rather great in this respect. In some species the shape of the shield is also described by stating if the shield narrows more or less anteriorly, if the lateral margins are rounded or straight, and if antero-lateral angles are present. The configuration of the rostral margin of the shield: the rostral margin is either broad or narrow, in each case broadly or narrowly rounded, with or without a distinct rostral angle, and is sometimes protracted in a short rostral process of varying form. The shape, direction, length and proportions of the cornua: These features seem to be rather unvarying within the species, and they are used constantly in the diagnoses for separating the different species; the length of the cornua is (after Stensiö) given in relation to the distance of their tips from the rostral end of the shield. A pectoral angle has not been found in the species described below. If present, it is only marked in the exoskeletal rim bordering the dorsal margin of the zonal part (in some instances its presence seems possibly to be explained as an imperfection in the preservation of that rim, cf. *C. borealis, C. acuticornis,* Stensiö 1927, pls. 1:3; 2:4). The presence or absence of denticles on the cornua: this is apparently a good specific character; the denticles must not be confused with long or pointed tubercles occurring as ornamentation on the outer face of the exoskeleton of the shield and thus also on the margins of the cornua (see e. g. *C. powriei,* p. 318). The shape and extent backwards of the inter-zonal part: the breadth (given in relation to the maximum breadth of the shield) is rather characteristic; the length seems to be somewhat variable; the extent backwards of the posterior angle in relation to that of the postero-lateral angles is used as a separating character; the height of the inter-zonal part is seldom noted as in most species it is rather inconsiderable, and as the specimens may be somewhat flattened dorso-ventrally the actual height cannot be positively stated and the varying state of preservation obscures the real differences. The absence or presence, size and shape of a dorsal ridge or spine on the interzonal part: these are features well characterizing the species; however, as constituting the highest point of the shield, this part is much subject to destruction during fossilization, and is thus often badly preserved or absent (see e. g. *C. signata,* p. 350). The shape and extent of the sensory fields: these are relatively constant characters, the dorsal field can, however, vary somewhat in shape (see *C. hyperboreus,* p. 306); the lateral fields are subject to some variations in their extent backwards on the cornua; the small indentations often seen in the median margins of the field are variable and of no differentiating value; in many species the lateral field is characteristically bent in the middle of its length in such a way that the posterior half of the field comes closer to the lateral margin of the shield than the anterior half. The size and position of the orbital openings: the size of the orbital openings in proportion to the size of the shield is sometimes a characteristic feature; the outer parts of the circum-orbital rim (when present) must, however, be completely preserved and representing the real margins of the orbital opening; when the circum-orbital ridge is abraded the "orbital opening" looks larger than it had actually been; the position of the orbital openings in relation to the rostral and the posterior end of the shield or, when the posterior parts of the shield are not preserved, to the pectoral sinus, is given, and this character seems to vary within rather narrow limits. The presence or absence of an independent pineal plate; the actual pineal plate, when present, is never preserved in the Spitsbergen material, but its presence is indicated by the pineal groove or fissure. The development and structure of the exoskeleton, its ornamentation, and the development of the mucous canal system, if enclosed in the exoskeleton: the development and the ornamentation of the exoskeleton can vary within the single species and must thus be used with caution as specific characters; in most cases, however, they seem to be rather constant; it must also be noted that the exoskeleton and its ornaments as well as the mucous canal system can be differently developed in different parts of the same shield and that when comparing these characters in different shields one must try to compare them in corresponding parts of the shields. The sensory line system: the characters from this system are not used as a specific character; when differences are seen in the species, they are probably most often due to failure in tracing the sensory lines as distinct grooves.

As will be seen from the descriptions of the species given below, rather many of the species are founded on a single specimen. This is done when the specimen exhibits distinct differentiating characters and the species seems not likely to be confused with other species. In such cases the diagnosis of the species is, of course, only preliminary. In many instances the material of the different species is furthermore too scanty to supply adequate information on the variability and the limits of the species. Also in these cases the diagnoses can only be said to be preliminary. Some of the species described below may possibly be proved in the future to be only forms of other rather variable species (see the remarks to *C. ibex* and *C. hastata, C. exilis* and *C. retusa);* with our present knowledge it seems in such cases better to separate the different forms that can be distinguished than to unite them into larger units.

Fifty-eight named species of the genus *Cephalaspis* are now known from Spitsbergen; seventeen of them were known to Stensiö in 1927 and thirty-nine are described as new in this paper. It must, however, be noted that in this paper I apply a much narrower conception of species than Stensiö, and that several of his species have been thought to be complex units and have accordingly been subdivided, each into two or more species.

Two of the Spitsbergen species originally placed in *Cephalaspis* have been transferred to other genera, viz. *C. staxrudi,* which, as already mentioned by Stensiö (1932, pl. 160; cf. Säve-Söderbergh 1941b, p. 239, footnote; Denison 1951a, pp. 159, 191), belongs to *Securiaspis,* and *C. kolleri,* which is now placed in the new genus *Tegaspis.*

For comparison I shall give below an enumeration also of the species of *Cephalaspis* known from other countries. From Great Britain twenty-two species are described (see Stensiö 1932; White 1935b), and from Canada eight species (Lankaster 1870b; Whiteaves 1881; Traquair 1890, 1893; Robertson 1936, 1937), two species are known so far from Podolia (Zych 1937; Paucă 1941) and one species from Germany (Gross 1933a). Two specimens, inappropriately attributed to *C. lyelli,* are recorded from Northern France by Leriche (1906, p. 37; cf. Stensiö 1932, p. 122). One species is described from the United States (Bryant 1933), but is too imperfectly preserved to allow a definite generic determination. One species described as a *Cephalaspis* species *(C. oeselensis)* from the Isle of Saaremaa (Robertson 1939b), although imperfectly known, does certainly not belong to this genus.[1]

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[1] The species is referred by Denison (1951a, pp. 159, 191) to a new genus, for which the name "*Procephalaspis*" is proposed; this name is, however, not valid according to the Int. Rules of zool. Nomenclature, Art. 23c.

The species hitherto recognized (and named) in the genus *Cephalaspis,* their provenience and geologic age are as follows:

From Great Britain (starting from the revision by Stensiö 1932):

C. acutirostris Stensiö	(Dittonian)	
C. agassizi Lank.	,,	
C. cradleyensis Stensiö (also in Spitsbergen)	,,	
C. fletti Stensiö	,,	
C. heightingtonensis Stensiö	,,	
C. jacki White	,,	
C. langi Stensiö	,,	
C. lankesteri Stensiö	,,	
C. lornensis Traq.	,,	(?)
C. lyelli Ag.	,,	(?)
C. magnifica Traq.	(Mesodevonian)	
C. pagei Lank.	(Dittonian?)	
C. powriei Lank. (also in Spitsbergen)	(Dittonian?)	
*C. salwey*i Egert.	,,	
C. sollasi Stensiö	,,	
C. spinifer Stensiö	,,	(?)
C. traquairi Stensiö	,,	(?)
C. watsoni Stensiö	,,	(?)
C. websteri Stensiö	?	
C. whitbachensis Stensiö	(Dittonian)	
C. whitei Stensiö	,,	
C. woodwardi Stensiö[1]	,,	(?)

From Podolia (very probably Dittonian, see p.   ):

C. bucovinensis Paucă

C. kozlowskii Zych

From Germany (Siegenien):

C. diensti Gross

From Canada:

C. acadica Roberts.	(Eodevonian?)
C. campbelltonensis Whiteaves	"
C. canadensis Roberts.	"
C. dawsoni Lank.	"
C. jexi Traq.	(Eodevonian?)
C. laticeps Traq.	(Neodevonian)
C. patteni Roberts.	,,
C. rosamundae Roberts.	,,

From U.S.A. (Eodevonian):

C? wyomingensis Bryant

From Spitsbergen:

C. aarhusi n. sp.	(Dittonian)
C. acuminata n. sp.	,,
C. acuticornis Stensiö	(U. Eodevonian?)
C. apicalis Stensiö	(Dittonian)
C. arcticus Stensiö	,,
C. borealis Stensiö	(U. Eodevonian?)
C. brevicornis Stensiö	,,
C. broughi n. sp.	(Dittonian)
C. caroli n. sp.	(U. Eodevonian)
C. corystis n. sp.	(Dittonian)
C. cradleyensis Stensiö (also in Great Britain)	,,
C. crofti n. sp.	,,
C. curta n. sp.	(U. Eodevonian)
C. deltoides n. sp.	(Dittonian)
C. dissimulata n. sp.	,,

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[1] With our present knowledge of the species and of the genus *Cephalaspis* in general the transfer of this species to a new genus *("Stensiopelta";* not valid name; Denison 1951a, pp. 159, 191) is unwarranted.

C. divaricata n. sp.	(Dittonian)
C. doryphorus n. sp.	,,
C. eukeraspidoides Stensiö	,,
C. eurhynchus n. sp.	,,
C. eurynotus n. sp.	,,
C. excellens n. sp.	,,
C. exilis n. sp.	,,
C. føyni n. sp.	,,
C. fracticornis n. sp.	(U. Eodevonian)
C. gracilis Stensiö	(Dittonian)
C. gigas n. sp.	(U. Eodevonian?)
C. hastata n. sp.	(Dittonian)
C. heintzi Stensiö	,,
C. høegi Stensiö	(U. Eodevonian?)
C. hoeli Stensiö	(Dittonian)
C. hyperboreus n. sp.	,,
C. ibex n. sp.	,,
C. isachseni Stensiö	(Siegenian)
C. jarviki n. sp.	,,
C. lanternaria n. sp.	(U. Eodevonian?)
C. lata Stensiö	,,
C. laticornis Stensiö	(U. Eodevonian)
C. menoides n. sp.	(U. Eodevonian?)
C. metopias n. sp.	(Dittonian)
C. moy-thomasi n. sp.	(U. Eodevonian?)
C. oblonga Stensiö	(U. Eodevonian)
C. oreas n. sp.	(Dittonian)
C. pinnifera n. sp.	,,
C. platycephalus n. sp.	,,
C. powriei Lank. (also in Great Britain)	,,
C. producta n. sp.	(U. Eodevonian)
C. pygmaea n. sp.	(Dittonian)
C. recticornis n. sp.	,,
C. retusa n. sp.	,,
C. semicircularis n. sp.	(U. Eodevonian?)
C. signata n. sp.	(Dittonian)
C. sinuata n. sp.	,,
C. spitsbergensis Stensiö	,,
C. tenuicornis n. sp.	,,
C. verruculosa n. sp.	,,
C. vogti Stensiö	,,
C. watneliei Stensiö	(Siegenian)
C? pedata n. sp.	(Dittonian)

The number of species will certainly increase considerably in future. There are for instance many species from Podolia not yet described (Zych 1937, pp. 50—51), and in the collections from Spitsbergen there are many remains, probably belonging to *Cephalaspis,* which are on one side too fragmentary to be described as new species but on the other hand too differently shaped as to be placed in any of the known species. These fragments thus indicate that here the fauna is still richer in *Cephalaspis* species than is apparent from the following account.

As to the geologic range of the genus it may be noted that *Cephalaspis* is not known from horizons older than the Dittonian; the youngest species come from layers (in Canada) of a Lower Neodevonian age.

Almost all the species from Spitsbergen are geographically confined to this faunal area, and only two species are previously known from another area, viz. *C. cradleyensis* and *C. powriei,* which occur also in Great Britain.

Among the Spitsbergen *Cephalaspis* species some groups of species, which are apparently very closely related to each other, can be distinguished. The following species can be placed together in different groups. *C. excellens* and *C. vogti* are, as mentioned above, closely akin, and form a very distinct species group, which is possibly related to *C. hyperboreus.* A second group of similar species is formed by *C. hoeli, C. exilis, C. retusa,* and *C. dissimulata* (all formerly included in *C. hoeli); C. eukeraspidoides* may also belong here. *C. corystis,* *C. hastata, C. ibex,* and *C. isachseni* are closely related, and constitute a separate species group, to which also *C. signata* may belong. A further group is formed by *C. sinuata, C. tenuicornis, C. verruculosa* and possibly also *C. arcticus* and *C. crofti. C. laticornis, C. semicircularis, C. menoides,* and *C. moy-thomasi* may belong to another species group, and, finally, the species *C. caroli, C. høegi, C. gigas, C. lanternaria,* and possibly *C. lata,* which evidently all are nearly related, constitute one group, probably closely akin to the preceding group. The two last mentioned groups, when better known, could possibly turn out to be related to *C. pinnifera.* An imperfectly known species, provisionally placed in *Cephalaspis (C? pedata)* may possibly be a transitional form to the genus *Tegaspis.* Some of the remaining species may be closely allied to each other but do not seem to belong to distinct species groups. Their supposed relatives are mentioned in the remarks on the separate species. Other species may belong to any of the above-mentioned groups but are too imperfectly known as to allow a definite statement in this respect. Some species seem to stand rather isolated systematically (e. g. *C. recticornis, C. doryphorus, C. metopias).*

A. Species from the Red Bay series (spp. 1—35).

1. *Cephalaspis aarhusi* n. sp.

(Fig. 23; pl. 1:1.)

Diagnosis. — A *Cephalaspis* species of fairly large size with maximum breadth of cephalic shield nearly one and a half times as great as length of shield in median line. Rostral end of shield narrow, without rostral angle. Cornua fairly stout and rather long, projecting in posterior and slightly lateral direction; their length equalling about one-third of distance of their tips from rostral end of shield. Inner margin of cornua without denticles. Pectoral sinus rather broad and shallow. Inter-zonal part short and rather narrow, its breadth being contained about three times in maximum breadth of shield. Dorsal sensory field small, about twice as long as broad. Lateral sensory fields narrow anteriorly, rather broad in posterior half, reaching backwards on to middle parts of cornua. Orbital openings small; distance of orbit from rostral end of shield and from pectoral sinus about equal. Small independent pineal plate probably present. Outer parts of exoskeleton subdivided into polygonal areas by narrow circum-areal mucous grooves. Outer face of exoskeleton in major part of shield smooth; small tubercles on zonal part. Mucous canal system situated in circum-areal grooves and in intra-areal canals. Polygonal areas small in proportion to size of shield.

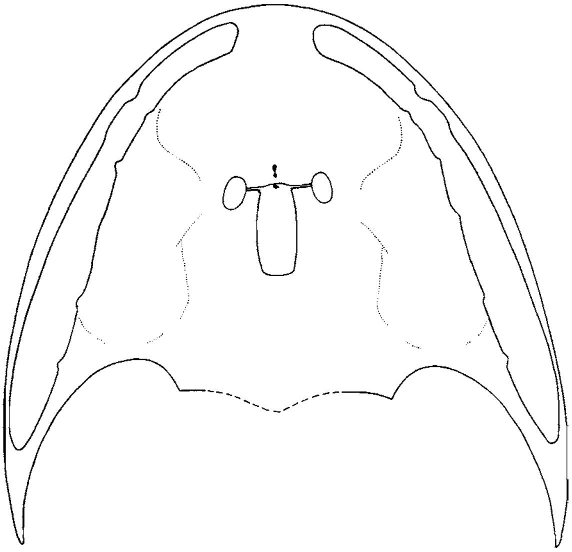


Fig. 23. — *Cephalaspis aarhusi* n. sp. Restoration of the cephalic shield in dorsal view. After the holotype (ENS no. 487). ½.

Holotype. — Cephalic shield (ENS no. 487).

Material. — The material referable to this species consists of the holotype only, an imperfect cephalic shield, partly in counterpart, lacking the left cornu and adjacent parts as well as a small dorso-median portion of its inter-zonal part.

Description. — The dimensions of the holotype are as follows: The length of the cephalic shield in the median line is estimated at maximally 11 cm; the distance of the tip of the cornu from the rostral is about 15.6 cm; the maximum breadth of the shield, which lies between the middle parts of the cornua, is estimated at about 15 cm; the breadth of the inter-zonal part between the postero-lateral angles is 5.6 cm; the distance of the pineal fissure from the rostral end of the shield is 5.1 cm; the height at the posterior end of the preserved portion of the inter-zonal part is estimated at about 3.5 cm. The species had thus attained a rather large size.

Taken as a whole the cephalic shield is moderately broad, the maximum breadth, however, exceeding not inconsiderably or, more precisely, nearly one and a half times the length in median line; the anterior half of the shield is rather narrow, and also the inter-zonal part is narrow. The shield slopes gently and almost uniformly from the posterior end of the dorsal sensory field to the rostral end of the shield.

The rostral margin is sharply rounded but certainly without any rostral angle; it passes imperceptibly into the slightly convex lateral margins. The cornua, which project in a posterior and slightly lateral direction, reach backwards far behind the posterior end of the shield; their length is contained three times in the distance of their tips from the rostral end of the shield. The cornua are rather stout and broad in their proximal part but taper rapidly to the slender and somewhat more straightly posteriorly directed distal part; they are much flattened dorso-ventrally. The inner margins of the cornua are devoid of denticles. The pectoral sinus are rather well defined but broad and shallow, uniformly concave without any antero-median or antero-lateral corner; in shape they rather much resemble those of *C. lankesteri*. The inter-zonal part is short; its breadth between the postero-lateral angles is only slightly more than one-third of the maximum breadth of the shield; it is comparatively high; the most dorsal part is not preserved but it seems very likely that there had been a median dorsal ridge; whether this ridge continued posteriorly as a dorsal spine, or not, can, however, not be determined. The dorsal sensory field is comparatively small, about twice as long as broad with truncated anterior and posterior margins; its anterior margin lies immediately behind the pineal fissure; the distance of the posterior margin of the field from the posterior end of the inter-zonal part is not exactly known, but is in any case greater than the length of the field. The lateral sensory fields are narrow in their anterior extremity, and gently increasing in breadth backwards with the greatest breadth at about the level of the anterior border of the pectoral sinus; backwards they reach to about the middle of the length of the cornua (as seen on the counterpart). The distance between the antero-median margins of the two lateral fields is rather small, and about equal to the inter-orbital breadth. The orbital openings are small, oval in shape, with their main axes convergent anteriorly; they are situated slightly in front of the middle of the length of the shield in the median line, and their distance from the rostral end of the shield is as great as that from the pectoral sinus. The circum-orbital ridge is rather low and continuous anteriorly with a feebly marked antorbital prominence. Between the orbital openings there is a very narrow transverse slit (fissura pinealis) in the exoskeleton; the fissure widens rather abruptly in its median part, which probably was occupied in the living animal by a small independent pineal plate. The naso-hypophyseal opening is very small; the circum-nasal fossa is very shallow and ill-defined, with the exception of its anterior part, which forms a rather deep, well marked quadrangular cavity lodging the anterior division of the naso-hypophyseal opening.

The exoskeleton is well developed. The superficial layer probably forms a continuous covering to the middle layer in each polygonal area; it is, as far as can be seen, smooth, without any ornamentation, only at the inner border of the pectoral sinus there are some small, blunt tubercles. The middle layer has well developed radiating canals of extremely small calibres. The basal layer contains small ringsinus. The mucous canal system was only partly enclosed in the exoskeleton, it was lodged in open circum-areal grooves and in small intra-areal canals. The polygonal areas are small in proportion to the size of the shield; they vary somewhat in size, being markedly smaller in the vicinity of the circum-nasal fossa and anteriorly to it; the average diameter of the polygonal areas elsewhere on the shield is 1.8 mm.

Of the sensory line system some narrow grooves are observed (cf. fig. 23). A short oblique line near the median margin of the posterior part of the lateral sensory field possibly belongs to the extra-lateral line.

The endoskeleton seems to be rather poorly ossified but very little of it is exposed, viz. some of the canals in the lateral sensory field.

Remarks. — This species, which is named in honour of Mr. Stig Aarhus, Oslo, a member of the ENS expedition in 1939, is rather suggestive of some of the *Cephalaspis* species from Great Britain, viz. *C. salweyi, C. lankesteri* and *C. whitbachensis* (cf. Stensiö 1932, pp. 90, 123, 131). It attains about the same size as *C. salweyi* but differs from that species in the shape of the inter-zonal part, the cornua and the sensory fields. From *C. lankesteri* and *C. whitbachensis* it is at first sight distinguished by the size of its shield, being about twice as great as in these species; furthermore from *C. lankesteri,* which it resembles in the shape of the cornua and pectoral sinus, it differs in the shape of the sensory fields and in the minute structure of the exoskeleton, and from *C. whitbachensis* in the somewhat different shape of the cornua and the pectoral sinus, as also in the shape of the sensory field and in the disposition of the mucous canal system. *C. aarhusi* shows no very close resemblance to any of the other *Cephalaspis* species from Spitsbergen.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Ben Nevis division.

Locality. — Spitsbergen, E. side of Red Bay: Mt Ben Nevis, in talus.

The specimen was collected by the ENS expedition in 1939.

2. *Cephalaspis cradleyensis* Stensiö.

(Fig. 24; pl. 2)

1932. *Cephalaspis cradleyensis,* Stensiö, pp. 130—131; fig. 44; pl. 15:6.

Diagnosis. — A *Cephalaspis* species of small size with maximum breadth of cephalic shield about as great as length of shield in median line. Shield somewhat narrowing anteriorly. Rostral angle present. Lateral margins slightly rounded. Cornua rather short, projecting in posterior and somewhat lateral direction, reaching backwards only somewhat behind posterior end of inter-zonal part; their length contained about four times in distance of their tips from rostral end of shield. Inner margins of cornua with denticles. Pectoral sinus

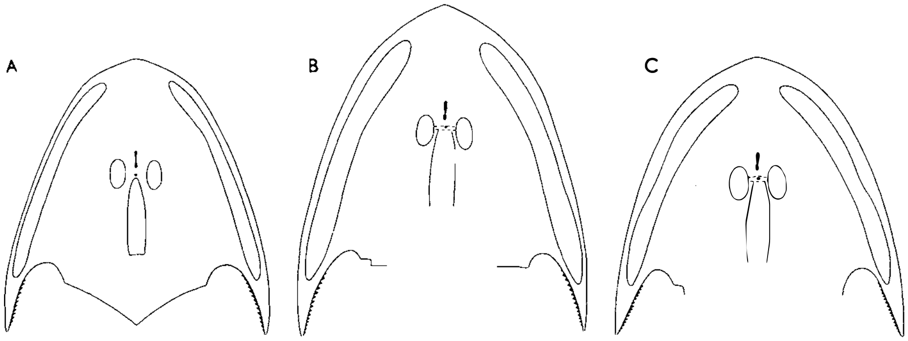


Fig. 24. — *Cephalaspis cradleyensis* Stensiö. A, restoration of the cephalic shield, based on the Spitsbergen specimen (Pal. Mus. Oslo no. A30024); B, C, attempted restorations after Stensiö (1932, fig. 44), based on the holotype. Nat. size.

narrow and moderately deep. Inter-zonal part moderately short and rather broad; its breadth contained about twice in maximum breadth of shield; dorsally provided with a low indistinct median ridge. Posterior angle of inter-zonal part protracted backwards somewhat behind postero-lateral angles. Dorsal sensory field narrow, about three and a half times as long as broad. Lateral sensory fields reaching backwards over basal parts of cornua. Orbital openings oval in shape, situated in front of middle of length of shield in median line. Exoskeleton on rostral and lateral margins and near pectoral sinus of shield ornamented with numerous small, flat tubercles. Superficial layer (probably) continuous. Mucous canal system (probably) enclosed in exoskeleton (after Stensiö 1932, p. 130; altered).

Holotype. — Cephalic shield (no. P.5375) in the British Museum (N.H.), London (Stensiö 1932, p. 130).

Material. — To this species is referred only one specimen (Pal. Mus. Oslo no. A30024). It consists of a fairly complete cephalic shield in counterpart, showing the general aspect of the shield; both the exoskeleton and the endoskeleton are, however, poorly preserved.

Description. — In the following the Spitsbergen specimen is described. The length of the shield in median line is 35.5 mm; the maximum breadth, which lies near the tips of the cornua, is estimated at 36 mm. the breadth of the inter-zonal part between the postero-lateral angles is 19.7 mm; the distance of the tip of the left cornu from the rostral end of the shield is 40.5 mm; the distance of the pineal foramen from the posterior end of the shield is 19 mm, and from the rostral end 16 mm. The present specimen is thus only slightly smaller than the holotype.

The cephalic shield is narrow, and its maximum breadth is about equal to the length of the shield in the median line and slightly less than the distance of the cornual tips from the rostral end of the shield. The shield is moderately narrowing in breadth towards the rostral end.

The rostral margin is fairly narrow and is marked off from the lateral margins by distinct but very obtuse antero-lateral angles. A rostral angle is present. The lateral margins are only slightly rounded. The cornua, which project in posterior and somewhat lateral direction, are flattened, rather narrow and straight and fairly short; their length constitutes only about one-fourth of the distance of their tips from the rostral end of the shield; they reach backwards to a point some little distance behind the posterior end of the inter-zonal part. The outer margins of the cornua are slightly more curved than the inner margins; the latter are provided with small anteriorly inclined denticles. The pectoral sinus are moderately shallow and rather narrow; they are almost uniformly concave. The inter-zonal part is rather short but comparatively broad, its breadth between the postero-lateral angles is only somewhat more than one-half of the maximum breadth of the shield. The posterior angle is protracted backwards to a point some distance behind the postero-lateral angles. Dorsally the inter-zonal part is provided with a low, rather indistinctly defined dorsal ridge, which seems to be highest in the middle of its length and thus fading away anteriorly towards the posterior end of the dorsal sensory field and posteriorly towards the posterior end of the inter-zonal part. The dorsal sensory field is narrow, its length being about three and a half times as great as its breadth; the posterior margin is abruptly truncated, whereas anteriorly the field is gently narrowing. The distance of the posterior margin of the field from the posterior end of the inter-zonal part is somewhat shorter than the length of the field itself. The lateral sensory fields reach backwards only to the basal parts of the cornua and are thus somewhat shorter than in the holotype. The orbital openings are moderately large, and oval in shape; they are situated distinctly nearer to the rostral than to the posterior end of the shield, and their distance from the former is about equal to that from the pectoral sinus. The orbital openings are rather close to each other, the inter-orbital breadth being less than one and a half times as great as the transverse diameter of an orbital opening. The inter-orbital space is imperfectly preserved and it is not possible to decide whether there was an independent pineal plate or not.

The exoskeleton is very imperfectly preserved. Along the lateral margin of the shield it is ornamented with low, flattened, and lengthened tubercles; on the dorsal side of the shield the outer face of the exoskeleton seems to be fairly smooth without any tubercles. The radiating canals are very delicate. The mucous canal system is in all probability entirely enclosed in the exoskeleton but nothing definite can be said about its development.

Of the endoskeleton only some faint traces of the superficial canals for nerves and veins are observed; the first nerve canal for the lateral sensory field and the vein canal vls_3 seem to be disposed as normally in the genus.

Remarks. — The specimen described above, although imperfectly preserved in many respects, agrees in almost all observable details with the holotype of *C. cradleyensis,* and can thus safely be assigned to that species. The original description was based on a very limited material, viz. one specimen only, and this specimen consisted in its turn of an imperfect and distorted cephalic shield. Two alternative attempts at restoration of the shield were thus made by Stensiö (cf. fig. 24B, C), one (B) made mostly after the right side, the other (C) mostly after the left side of the specimen. The restoration made after the Spitsbergen specimen (fig. 24A) agrees in its general shape better with the first one of Stensiö's restorations but is somewhat broader and more narrowing anteriorly just as in the second of Stensiö's restorations. From the present specimen the shape of the inter-zonal part and the dorsal field, previously rather uncertain, have been brought to light; in other respects, however, i. a., as regards the structure of the exoskeleton, the species is still imperfectly known.

The discovery of this species, described from the Dittonian of England, in the lower part of the Red Bay series in Spitsbergen, is very remarkable, both from a zoogeographical and from a stratigraphical point of view (cf. 580).

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Plant horizon.

The single specimen was collected by Th. Vogt's expedition in 1928.

3. *Cephalaspis acuminata* n. sp.

(Fig. 25; pl. 3).

Diagnosis. — A rather small *Cephalaspis* species with maximum breadth of cephalic shield slightly greater than length of cephalic shield in median line. Anterior part of cephalic shield narrow; rostral margin narrow, with rostral angle. Cornua rather long, projecting in posterior direction and reaching far behind posterior end of inter-zonal part, slightly curved in medial direction; their length contained about two and a half times in distance of their tips from rostral end of shield. Inner margin of cornua with small, triangular, antero-medially directed denticles. Pectoral sinus narrow and rather deep. Inter-zonal part comparatively long; its breadth constitutes nearly two-fifths of maximum breadth of cephalic shield; dorsally with rather high, slightly posteriorly inclined median spine. Dorsal sensory field elongate with slightly curved lateral margins. Lateral sensory fields reaching backwards on cornua but ending before middle of their length. Orbital

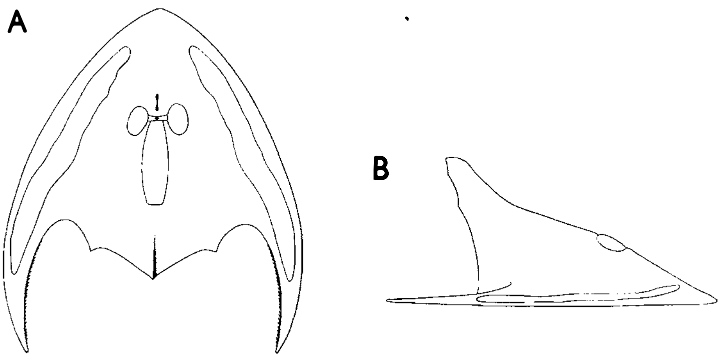


Fig. 25. — *Cephalaspis acuminata* n. sp. Restoration of the cephalic shield A, in dorsal view, B, in lateral view. Mainly after the holotype (Pal. Mus. Oslo no. A30025), About nat. size.

openings situated nearer to rostral than to posterior end of shield. Independent pineal plate present. Exoskeleton ornamented with minute tubercles; superficial layer continuous.

Holotype. — Cephalic shield (no. A30025) in the Palaeontological Museum, Oslo.

Material. — The material, which can be placed in this species with a fair degree of certainty, consists of five specimens (Pal. Mus. Oslo nos. A30025—A30027 and ENS nos. 488—489). In addition to these specimens I have also placed here, though with hesitation, one specimen, ENS no. 490. No. A30025, the holotype (pl. 3), consists of a complete cephalic shield, in counterpart; the other specimens consist only of more or less fragmentary shields.

Description. — The dimensions of the holotype shield are the following: The length in the median line (from the rostral end to the posterior end of the inter-zonal part at the basis of the dorsal spine) is 33.7 mm; the maximum breadth (which in the holotype lies between the middle parts of the cornua) amounts to 36.5 mm; the distance of the tip of the left cornu from the rostral end of the shield is 46 mm; the breadth of the inter-zonal part between the postero-lateral angles is 16.2, and the height of the shield at the posterior end of the inter-zonal part (the dorsal spine not included) about 12 mm. In no. 489 the length of the shield in the median line is 36 mm. The distance of the right cornu from the rostral end of the shield is in the remaining specimens 46 mm (no. A30026), 45 mm (no .A30027), 41.2 mm (no. 488) and about 38 mm (no. 490). The distance of the pineal fissure from the rostral end of the shield is about 16 mm (no. A30026), 18.3 mm (no. A30027), and about 14.5 mm (no. 488). The shields are all rather small and the species thus attained only a small size.

In general shape the cephalic shield is characterized by its narrowness; the maximum breadth, which lies between the middle or the distal parts of the cornua, is only slightly greater than the length in the median line and about four-fifths of the distance of the cornual tips from the rostral end of the shield. The anterior, pre-orbital, part of the shield is narrow and pointed, and the rostral margin is somewhat protracted and provided with a more or less well developed and distinct rostral angle, in the holotype somewhat rounded at the very apex. The lateral margins of the shield are slightly convex, and the lateral margins of the main shield pass imperceptibly into the rostral margin and into the lateral margins of the cornua. The cornua, which project in a posterior direction and reach far backwards behind the posterior end of the inter-zonal part, are rather long, and often in their distal parts slightly curved medially. The length of the cornua constitutes about two-fifths of the distance of their tips from the rostral end of the shield. The inner margins of the cornua are provided with small, narrowly triangular, antero-medially directed, slightly curved denticles. The pectoral sinus are well defined, rather narrow and deep; in no. 488 they are, however, rather shallow; in no. A30027 there is a rather distinct antero-medial corner in the right pectoral sinus but in the other specimens the sinus are almost uniformly concave. The inter-zonal part is rather long and its breadth between the postero-lateral angles is contained about two and a half times in the maximum breadth of the shield. The inter-zonal part is very high in proportion to its breadth; its height at the posterior end (the dorsal spine excluded) constitutes about three-quarters of its breadth. Dorsally the inter-zonal part is provided with a rather high median spine, which is slightly inclined posteriorly; the spine is not acuminate but has a rather truncated apex. The posterior end of the inter-zonal part at the basis of the dorsal spine is protracted backwards for some distance behind the postero-lateral angles. The sensory fields are well developed. The actual shape of the dorsal field is not revealed in the holotype nor to its full extent in any of the other specimens; but from what is preserved of the field in the different specimens its shape can be restored as shown in fig. 25A. The dorsal field is thus elongate and at most three times as long as broad with its broadest part in the middle of its length and with slightly curved lateral margins; its anterior margin, which lies immediately behind the pineal groove is abruptly truncated, and it is very probable that also the posterior margin was truncated or only slightly rounded. The distance of the posterior margin of the field from the posterior angle of the shield is probably only slightly less than the length of the field itself. The lateral sensory fields are moderatly broad and reach backwards on to the cornua but do not extend to their distal parts. The distance between the antero-medial ends of the two lateral fields is more than twice as great as the inter-orbital breadth. The orbital openings and the adjacent parts of the dorsal side of the shield are not exposed in the holotype and in no. 489, and only partly in the other specimens; they are of moderate size and oval in shape; it is evident that in the holotype and in no. 489 they are situated nearer to the rostral end than to the posterior end of the shield; in the other specimens the posterior portion of the inter-zonal part is not preserved and it is thus impossible here to determine exactly the position of the orbital openings; it seems, however, likely that they are not situated so far anteriorly as in the holotype. In nos. A30026—A30027, 488 the distance of an orbital opening from the rostral end of the shield is slightly greater than from the pectoral sinus of its side. The antorbital prominence is well developed in nos. A30026 and A30027. In these specimens the shape of the circum-nasal fossa is displayed, which is rather narrow, triangular, well defined and rather deep anteriorly. The presence in the living animal of an independent pineal plate is indicated by the pineal fissure.

The exoskeleton is apparently rather poorly preserved and its outer parts are furthermore not well exposed for investigation in any of the specimens with the exception of no. 490, hesitatingly placed in this species. The superficial layer is continuous and smooth or ornamented with very minute, low tubercles. The middle layer is provided with radiating canals, disposed, at least in the holotype, in rather irregular bundles, and the vascular areas are not well defined. The basal layer in the shield proper contains no ringsinus; in the inter-zonal part, however, there are observed very narrow ringcanals, encircling polygonal areas of rather irregular shapes. The mucous canal system is enclosed in the exoskeleton and consists of a network of canals of very small calibres.

The endoskeleton is well ossified and several of the internal structures are seen. With regard to the disposition of the superficial canals for nerves and vessels it can be noted that the canals of the nerves for the lateral sensory fields are developed as normally in the genus, that the vein canals vls_3 and vls_4 unite into a common trunk, which opens into the postero-dorso-lateral corner of the orbit and that the canals vls_5 and vls_6 also unite into a common trunk before opening into the canal *vcl.* The two trunks are anastomosing with each other by means of a rather wide sinuslike canal.

Remarks. — In the general shape of its shield *C. acuminata* is rather suggestive of *C. websteri* (Stensiö 1932, p. 133) from Great Britain; it differs, however, from that species in the smaller size of its shield, the deeper and narrower pectoral sinus, the shape of the cornua and also in the shape of the dorsal spine of the inter-zonal part. Among the Spitsbergen *Cephalaspis* species, *C. acuminata* resembles to some extent *C. eukeraspidoides* (p. 302; Stensiö 1927, pp. 267—268) and *C. føyni* (p. 265); from the first species it differs i. a. by the narrow shield, the broader inter-zonal part, the shorter cornua, and the narrower pectoral sinus, from the latter species by the greater size, the shape of the anterior part of the shield, the shape of the cornua and the inter-zonal part etc. (cf. also *C. producta,* p. 390).

Geological horizons. — Lover Eodevonian (Dittonian): Red Bay series, the Corvaspis horizon, the Primaeva horizon (and ? the Anglaspis horizon).

Localities. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, the Corvaspis horizon (no. 489); the Primaeva horizon (nos. 488, A30025 — A30027); the Anglaspis horizon (no. 490, hesitatingly placed in this species).

The specimens nos. A30025 — A30027 were collected by Th. Vogt's expedition in 1928, nos. 488—490 by ENS expedition in 1939.

4. *Cephalaspis eurhynchus* n. sp.

(Fig. 26; pls. 4; 5:5-6.)

Diagnosis. — A rather small *Cephalaspis* species with maximum breadth of cephalic shield about one and a quarter times as great as length of shield in median line. Anterior end of cephalic shield protracted into well developed broad rostral process. Lateral margins rather strongly convex. Cornua well developed, projecting in posterior direction, reaching far behind posterior end of inter-zonal part; distinctly curved medially. Length of cornua contained somewhat more than two and a half times in distance of their tips from rostral end of shield. Inner borders of cornua with long, closely set denticles. Pectoral sinus rather narrow. Inter-zonal part short and broad, its breadth constituting half of maximum breadth of shield. Posterior angle very obtuse, protracted backwards only slightly behind postero-lateral angle. Dorsal sensory field elongate, probably slightly more than twice as long as broad, in anterior part rapidly narrowing towards pointed anterior end. Lateral fields rather narrow, reaching backwards to proximal parts of cornua. Orbital openings fairly large, roundedly oval in shape, situated about midway between rostral and posterior ends of shield. Independent pineal plate present. Superficial layer of exoskeleton continuous. Radiating vascular canals well developed, disposed in distinct bundles. Mucous canal system enclosed in exoskeleton, forming a rather fine-meshed network.

Holotype. — Cephalic shield (no. A30030) in the Palaeontological Museum, Oslo.

Material. — To this species I refer three specimens, Pal. Mus. Oslo nos. A30028 — A30030. The holotype (no. A30030; pl. 4) consists of a cephalic shield with counterpart, lacking a dorso-median portion of the inter-zonal part and the right cornu. No. A30029

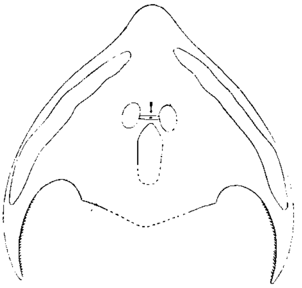


Fig. 26. — *Cephalaspis eurhynchus* n. sp. Restoration of the cephalic shield in dorsal view (based on Pal. Mus. Oslo nos. A30028—A30030). Nat. size.

(pl. 5:6) consists of a rather complete cephalic shield, partly in counterpart while no. A30028 (pl. 5:5) consists of a cephalic shield lacking a considerable portion of its central and posterior parts. In addition to these specimens I place here with some hesitation a specimen (ENS no. 491), which consists of the antero-medial portion only of a cephalic shield.

Description. — The dimensions (in mm) of the cephalic shields are given in the following table (figures in brackets are only approximate).

Nos.	A30028	A30029	A30030
Length in median line	—	(27)	(30)
Maximum breadth	31	34	(37)
Distance of tip of cornu from rostral end of shield	33.5	39.4	42
Distance of postero-lateral angles of inter-zonal part from rostral end of shield	(23)	26.3	(29)
Breadth of inter-zonal part	(15)	15.5	(18)

The height of the shield could not be measured, but is in no. A30029 estimated at about 9 mm. The species in thus of small size, but somewhat variable in size and proportions of the shield.

In general shape the cephalic shield is rather broad; the maximum breadth, which lies across the middle parts of the cornua, is somewhat, and probably about one and a quarter times, greater than the length of the shield in the median line and slightly less than the distance of the tips of the cornua from the rostral end. The anterior end of the cephalic shield is protracted into a short and broad anteriorly rounded rostral process, which is marked off from the main cephalic shield by a distinct concavity at the transition of the rostral margin to the lateral margins. The length of the rostral process constitutes probably only one-seventh of the length of the whole shield in the median line. The lateral margins of the main shield are strongly curved and gradually and without any interruption passing into the lateral margins of the cornua. The cornua project in posterior direction and reach backwards far behind the posterior end of the inter-zonal part; their length constitutes about two-fifths of the distance of their tips from the rostral end of the shield. In shape the cornua are rather slender and somewhat flattened dorso-ventrally, and are distinctly curved in median direction. The cornual limb is provided with very closely set, rather long and thin, somewhat anteriorly curved and sharply pointed denticles. The pectoral sinus are comparatively broad, in proportion to the size of the shield much broader than in the probably related species *C. acutirostris* and *C. føyni;* they are rather shallow. The inter-zonal part is short but comparatively broad, its breadth between the postero-lateral angles is contained about twice in the maximum breadth of the shield. The postero-dorso-median portion of the inter-zonal part is not preserved in any of the specimens but, to judge from the shape of the preserved parts, the posterior end formed a very obtuse angle or was entirely rounded off; it was protracted backwards to a point only slightly behind the postero-lateral angles. The exact shape of the dorsal sensory field could not be ascertained as the field is not completely preserved; it is, however, seen that the anterior portion of the field is rapidly decreasing in breadth towards the anterior end which is distinctly pointed; the field was probably rather elongate and somewhat more than twice as long as broad. The lateral sensory fields are rather narrow, they extend backwards only on to the basal parts of the cornua, and are thus comparatively shorter than in *C. acutirostris* and *C. føyni;* the space between the antero-median ends of the two fields is about twice as great as the inter-orbital breadth. The orbital openings which are rather large in proportion to the size of the shield, are situated at about equal distances from the rostral and the posterior ends of the shield; they are roundedly oval in shape. The pineal foramen was placed in an independent pineal plate, which, however, is not preserved; the plate was situated somewhat in front of the dorsal sensory field. The circum-nasal fossa is well defined anteriorly, the anterior margin forms a distinct, slightly obtuse angle.

The exoskeleton is not well exposed for investigation and the minute structure of its outer parts is thus rather obscure. It seems, however, very probable that the superficial layer is continuous and that its outer face is either feebly ornamented or quite smooth. The radiating canals in the middle layer are well developed and disposed in distinct fascicles, emanating from groups of ascending canals, thus forming well defined vascular areas; the diameter of a vascular area is on the average 1.7 mm and thus comparatively large. Between the antero-median ends of the lateral sensory fields in no. A30029, there are two groups of ascending vascular canals and from these groups issue many parallel canals, running in straight anterior direction on to the rostral process. The basal layer contains no ringsinus. The mucous canal system is not differentiated into circum-areal and intra-areal canals but is developed as a uniform, rather fine-meshed plexus of not very fine-calibrated canals; it was very probably entirely enclosed in the exoskeleton.

The endoskeleton is very well ossified and several of the internal structures are seen, especially in no. A30030 (pl. 4). Here will only be mentioned that the first nerve canal for the lateral sensory field behaves as normally in the genus except on the left side of the shield in no. A30028, where it divides into two branches at a point about midway between the orbit and the lateral field (pl. 5:5), and that the canal vls_3 is isolated and does not join the canal vls_4 before it opens directly into the postero-dorso-lateral corner of the orbit; the proximal courses of the other dorso-lateral superficial vein canals could not be observed.

Remarks. — *Cephalaspis eurhynchus* is characterized by the rather broad cephalic shield, the pronounced rostral process, the broad inter-zonal part and the long, slender, medially curved cornua. In the shape of the anterior parts of its shield the species reminds somewhat of *C. acutirostris* (Stensiö 1932, p. 97), *C. føyni* and *C. broughi* (p. 268) but differs from these species, with which it is possibly related, principally in the shape of the comparatively broad shield and of the long and slender cornua.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the Primaeva horizon,? the Anglaspis horizon.

Localities. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Primaeva horizon (nos. A30028—A30030); in the Anglaspis horizon (no. 491, hesitatingly placed here).

The specimens nos. A30028—A30030 were collected during Th. Vogt's expedition in 1928, no. 491 during the ENS expedition in 1939.

5. *Cephalaspis føyni* n. sp.

(Fig. 27; pl. 5:4)

Diagnosis. — A small and narrow *Cephalaspis* species with maximum breadth of cephalic shield slightly less than length of shield in median line. Anterior end of shield protracted into short and broad rostral process. Cornua rather long, projecting in posterior direction and extending backwards far behind level of posterior angle of inter-zonal part; length of cornua contained almost three times in distance of their tips from rostral end of shield. Inner border of cornua with denticles. Pectoral sinus narrow and rather deep. Inter-zonal part broad; its breadth more than a half time as great as maximum breadth of shield; moderately long and high, its dorso-median part reaching

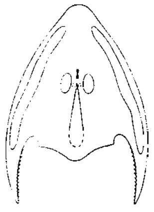


Fig. 27. — *Cephalaspis føyni* n. sp. Restoration of the cephalic shield in dorsal view. After the holotype (Pal. Mus. Oslo no. A30031). Nat. size.

farther backwards than postero-lateral angles. Dorsal sensory field very narrow in anterior part. Lateral sensory fields extending backwards on to basal parts of cornua. Orbital openings large, situated about midway between rostral and posterior ends of shield.

Holotype. — Cephalic shield (no. A30031) in the Palaeontological Museum, Oslo.

Material. — The species is based on the holotype (Pal. Mus., Oslo no. A30031) only; this is a somewhat defect cephalic shield.

Description. — The length of the cephalic shield in the median line is 19.8 mm, and the maximum breadth, which lies between the most basal parts of the cornua measures 18.5 mm. The breadth of the inter-zonal part posteriorly is 10 mm and the distance of the tips of the cornua from the rostral end of the shield 25 mm and 26.2 mm, respectively; the distance of the left postero-lateral angle of the inter-zonal part from the rostral end of the shield is 19 mm, and the distance of the supposed place of the pineal foramen from the rostral end of the shield 9.6 mm. The species was thus of a very small size.

The shield is long and very narrow, and the maximum breadth is even somewhat smaller than the length in the median line (a condition not met with in other *Cephalaspis* species) and constitutes about two-thirds of the distance of the tips of the cornua from the rostral end of the shield. The shield decreases in breadth rather evenly towards the rostral margin; the most anterior part of the shield is protracted into a broad and rather short rostral process, uniformly rounded anteriorly. There is a very slight concavity at the basis of the rostral process where the rostral margin passes over into the lateral margins of the shield; these latter margins are slightly rounded. The cornua which are rather long and slender, project in a posterior direction and reach backwards far behind the posterior end of the inter-zonal part. Their length constitutes slightly more than one-third of the distance of their tips from the rostral end of the shield. The distal parts of the cornua are curved slightly inwards; the basal parts are rather strongly flattened dorso-ventrally. The inner margins of the cornua are provided with small pointed, antero-medially directed, denticles. The pectoral sinus are narrow and rather deep, slightly asymmetrical with the greatest depth placed near the median margin. The inter-zonal part is not very long but comparatively high and rather broad; its breadth between the postero-lateral angles is more than a half time as great as the maximum breadth of the shield. The rounded posterior angle of the inter-zonal part reaches backwards to a point somewhat behind the postero-lateral angles. The dorso-median portion of the inter-zonal part is rather imperfectly preserved and it seems doubtful whether there was a dorsal median ridge or not; there was certainly no dorsal spine. The sensory fields are well developed but their exact shape is uncertain. The dorsal sensory field is long and narrow with its greatest breadth in the posterior part; anteriorly the field is gently narrowing towards its anterior end, the anterior portion of the field is thus very narrow. The lateral sensory fields extend backwards to the basal parts of the cornua. The orbital openings are large, oval in shape and situated at about the middle of the length of the shield in median line. Most of the interorbital space is not preserved in the specimen and nothing can be said whether there was an independent pineal plate or not. The development of the naso-hypophyseal opening and of the circum-nasal fossa are unknown.

The exoskeleton is very badly preserved and nothing can be said with certainty about its structure.

The endoskeleton is very imperfectly preserved, and only some traces of canals for superficial vessels and nerves can be seen.

Remarks. — *C. føyni* is named in honour of Mr Sven Føyn, director of the Geological Survey, Oslo, who was a member of the ENS expedition in 1939, and who has contributed much to our knowledge of the stratigraphy of the Old Red deposits in Spitsbergen. The species is easily distinguished from its congeners by the narrow cephalic shield, the short rostral process, the long, slender cornua and the shape of the dorsal sensory field. Among the Spitsbergen Cephalaspids *C. broughi* (p. 268), *C. eurhynchus* (p. 262), *C. deltoides* (p. 271) and *C. apicalis* (Stensiö 1927, p. 282) also have the shield anteriorly protracted into a somewhat similar rostral process. *C. føyni* differs from them all by its small size, from *C. eurhynchus* i. a. by the shape of the narrow shield, from *C. broughi,* which likewise has a narrow shield, by the comparatively much longer cornua, and from *C. apicalis* in the shape of the rostral process. *C. føyni* is somewhat suggestive of *C. acuticornis* (Stensiö 1932, p. 97) from the Dittonian of England, but is smaller, with longer cornua and a broader rostral process (cf. also *C. acuminata,* (p. 258).

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Vogti horizon.

Locality. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis [Northern part].

The single specimen was collected by Th. Vogt's expedition in 1928.

6. *Cephalaspis broughi* n. sp.

(Fig. 28; pl. 7).

Diagnosis. — A *Cephalaspis* species of medium size with maximum breadth of cephalic shield about equal to length of shield in median line. Anterior end of shield protracted into short, broad rostral process. Lateral margins slightly rounded. Cornua short, projecting in posterior direction and reaching backwards somewhat behind posterior end of inter-zonal part; their length contained four or five times in distance of their tips from rostral end of shield. Inner margins of cornua devoid of denticles. Pectoral sinus shallow. Inter-zonal part short, broad and fairly high; its breadth greater than one-half of maximum breadth of shield. Dorsal sensory field rather short, about twice as long as broad, with truncated anterior and posterior margins. Lateral sensory fields extending backwards to middle parts of cornua. Orbital openings oval in shape, situated behind middle of length of shield in median line. Superficial layer of exoskeleton continuous and (probably) without ornamentation. Mucous canal system enclosed in exoskeleton, differentiated into narrow circum-areal canals and intra-areal canals.

Holotype. — Cephalic shield (ENS no. 493).

Material. — The material, referable to this species, consists of two specimens (ENS nos. 492—493). The holotype (no. 493; pl. 7) is an imperfectly preserved cephalic shield in counterpart, lacking the postero-dorsal portion of the inter-zonal part and the distal parts of the cornua; the second specimen (no. 492) consists of a very imperfect cephalic shield in counterpart.

Description. — The dimensions of the cephalic shield in the holotype are as follows: The length of the shield in the median line cannot be directly measured but can be estimated at 77 mm. The maximum breadth, which probably was between the basalmost parts of the cornua, is estimated at 79 mm. The breadth of the inter-zonal part between its postero-lateral angles is 46 mm. The distance of the pineal opening from the rostral end of the shield is 47 mm, and the distance of the postero-lateral angles of the inter-zonal part from the rostral end of the shield is about 77 mm. The maximum height is estimated at about 28 mm disregarding the dorsal ridge, if there was one. The second specimen (no. 492) is too imperfectly preserved as to allow any direct measurements to be taken, but it seems to be only inconsiderably greater than the holotype.

Taken as a whole the shield is characterized by its narrowness with the maximum breadth being about as great as the length of the shield in the median line, and slightly less than the distance of the cornual tips

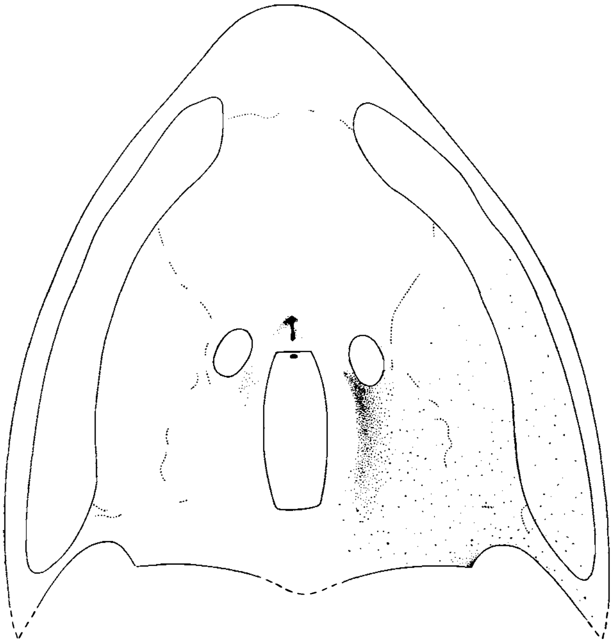


Fig. 28. — *Cephalaspis broughi* n. sp. Restoration of the cephalic shield in dorsal view. After the holotype (ENS no. 493). Nat. size.

from the rostral end of the shield. The anterior part of the shield is protracted into a broad, short, anteriorly uniformly rounded rostral process. There seems to be a very slight concavity in the antero-lateral margin of the shield at the transition from the rostral to the lateral margins. The lateral margins are somewhat rounded and the shield is gently narrowing towards the rostral margin. The cornua are not preserved in their very distal parts but, to judge from the direction of the lateral and median margins of the preserved parts, must have been projecting in a posterior direction, and been rather small, with a length constituting one-quarter or one-fifth of the distance of their tips from the rostral end of the shield. The cornua reach farther backwards than does the posterior end of the inter-zonal part. At least in the basal parts the cornua are flattened dorso-ventrally and their inner margins are devoid of denticles. The pectoral sinus are shallow and rather narrow. The inter-zonal part is rather high, short and broad, its breadth between the postero-lateral angles constitutes somewhat more than one-half of the maximum breadth of the shield. In the holotype and, to some extent also in no. 492, the inter-zonal part is imperfect dorso-medially yet to judge from the preserved parts in the latter specimen, the inter-zonal part was provided with a low, sharply defined dorsal median ridge. Whether this ridge continued posteriorly in a dorsal spine is uncertain but seems rather unlikely. The dorsal sensory field is bordered laterally by a rather broad flattened wall, which is well defined anteriorly, postero-medially to the orbits, but becomes rather indistinct posteriorly, towards the postero-lateral corners of the field; at the transition of the wall to the downward sloping sides of the shield a fairly well defined ridge is formed. The dorsal sensory field is rather small and narrow, about twice as long as broad; its lateral margins are very slightly curved and the anterior and posterior margins are truncated. The distance of its posterior margin from the posterior end of the shield is probably about half as great as the length of the field. The lateral sensory fields are comparatively broad with the maximum breadth at the beginning of the posterior quarter of the field; they reach backwards to the middle parts of the cornua. The distance between the antero-median margins of the two lateral fields is somewhat greater than the distance between the orbital openings. The latter are of a moderate size, and oval in shape; they are situated strikingly far back, and nearer to the posterior than to the rostral end of the shield. The pineal opening on the dorsal side of the endoskeleton lies within the dorsal sensory field close to its anterior margin; it seems reasonable to assume that there was a small independent pineal plate situated along the anterior margin of the field, and it is quite evident that the plate could not have reached laterally on to the orbital openings. The circum-nasal fossa is rather narrow, posteriorly indistinctly bounded.

The outer parts of the exoskeleton are rather imperfectly preserved and not well exposed for investigation so that nothing can be said with certainty about the development of the ornament of the outer face; it is however, evident that the ornamentation, if present, must have been rather feeble. The lower division of the middle layer has well developed radiating canals, forming very irregularly shaped vascular areas. The basal layer in no. 492 has irregular canals, but no regular ringsinus are developed. The mucous canal system is apparently enclosed in the exoskeleton; in the holotype it is developed as narrow circum-areal canals, enclosing polygonal areas of varying size and shape, and between them as a fine-meshed plexus of intra-areal canals.

The grooves of the sensory line system are well exposed in both specimens (the lines observed in the holotype are shown in fig. 28); it may be noted here that there is a short groove near the median margin of the posterior part of the lateral sensory field which must pertain to the extra-lateral line (cf. *C. signata,* fig. 51).

The endoskeleton seems to be well preserved but is on the whole not easily accessible for investigation.

Remarks. — This species is at once distinguished by the size and the general shape of its cephalic shield, and it cannot be confused with the other *Cephalaspis* species provided with a marked rostral process, viz. *C. acutirostris* (Stensiö 1932, p. 97), *C. føyni* (p. 265) and *C. eurhynchus* (p. 262). It is also evident that is cannot be identical with the very imperfectly known *C. apicalis* (Stensiö 1927, p. 282). — The species is named in honour of Professor James Brough, of University College, Cardiff, who is a well-known authority on fossil fishes, and who was a member of the ENS expedition to Spitsbergen in 1939.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Ben Nevis division.

Locality. — Spitsbergen. E. side of Red Bay: the Andrée Glacier, S. half, W. part, in the moraine.

Both specimens were collected by the ENS expedition in 1939.

7. *Cephalaspis deltoides* n. sp.

(Fig. 29; pl. 5:1-2.)

Diagnosis. — A *Cephalaspis* species of rather small size, with maximum breadth of cephalic shield almost twice as great as length of shield in median line. Anterior end of shield protracted into a very short, broad, anteriorly rounded rostral process. Lateral margins very slightly convex. Cornua very long and slender, projecting in postero-lateral direction and reaching backwards rather far behind posterior end of inter-zonal part; their length contained about twice in distance of their tips from rostral end of shield. Distal parts of cornua curved in posterior direction. Inner margins of cornua with few, hook-like denticles. Pectoral sinus broad and shallow. Inter-zonal part short; its breadth constituting about one-third of maximum breadth. Posterior angle very obtuse, rounded, projecting backwards only for some distance behind postero-lateral angles. Dorsal sensory field about twice as long as broad with slightly rounded lateral margins. Lateral sensory fields rather short, extending backwards over basal quarter of cornua. Orbital openings rather large, situated about midway between rostral and posterior end of shield. Independent pineal plate present. Ornamentation of exoskeleton consisting of very small tubercles. Mucous canal system not enclosed in exoskeleton.

Holotype. — Cephalic shield (ENS no. 494).

Material. — The material of this species consists of two specimens (ENS nos. 494—495). The holotype (no. 494, pl. 5:1-2) is represented by a fairly complete cephalic shield in counterpart, lacking the distal part of the right cornu. The second specimen (no. 495) consists of the incomplete half of a cephalic shield, exposed in ventral view.

Description. — The dimensions of the cephalic shield in the holotype are the following. The length in the median line is 41.7 mm and the maximum breadth, which lies between the distal parts of the cornua, is about 77 mm. The distance of the tip of the left cornu from the rostral end of the shield is 66.3 mm and the breadth of the inter-zonal part between the postero-lateral angles 24 mm. The distance of the pineal fissure from the rostral end of the shield is 20 mm. No. 495 seems to be slightly larger than the holotype, the distance of the rostral end of the shield from the pectoral sinus (the only dimension obtainable) is about 38 mm as against 35 mm in the holotype.

Taken as a whole the cephalic shield is triangular in shape, much depressed and broad, with a maximum breadth exceeding the median length nearly twice and also somewhat greater than the distance of the tips of the cornua from the rostral end of the shield.

The rostral end of the shield forms a very short and broad rostral process, the anterior margin of which is uniformly rounded without any distinct angle. The rostral process is only very indistinctly set off from the main shield by very slight concavities at the transition from the rostral to the lateral margins. The lateral margins are almost straight and form an angle of about 45 degrees with the main axis of the shield. The cornua project in the same direction and there are thus no boundaries at the lateral margins between the main shield and the cornua. The distal parts of the cornua are curved and directed almost straight backwards. The cornua are very long and slender and reach backwards far behind the level of the posterior end of the inter-zonal part. The length of the cornua constitutes about half the distance of their tips from the rostral end of the shield. The inner borders of the cornua are provided with only few rather large, anteriorly bent, hook-like denticles. The pectoral sinus are broad and rather shallow. The inter-zonal part is fairly short, and its breadth between the postero-lateral angles is contained about three times in the maximum breadth of the shield. The posterior margin of the inter-zonal part forms a very obtuse, rounded median posterior angle, which is protracted backwards only slightly behind the postero-lateral angles. The dorsal side of the inter-zonal part is provided with a low and rather indistinct median dorsal ridge. The dorsal sensory field is elongate and about twice as long as broad; its exact shape in the posterior parts is not visible but very probably it had the shape given in the restoration (fig. 29) and was thus almost rectangular in outline but with slightly convex lateral margins. The anterior margin of the field, which is truncated, lies immediately behind the pineal fissure and the distance of its posterior margin from the posterior end of the inter-zonal part is about equal to the length of the field. The lateral fields are comparatively short, of about the same shape as in *C. divaricata* and reach backwards only over the proximal parts of the cornua. The distance between the antero-median ends of the two lateral fields is about twice as great as the inter-orbital breadth. The orbital openings which are rather large in pro-

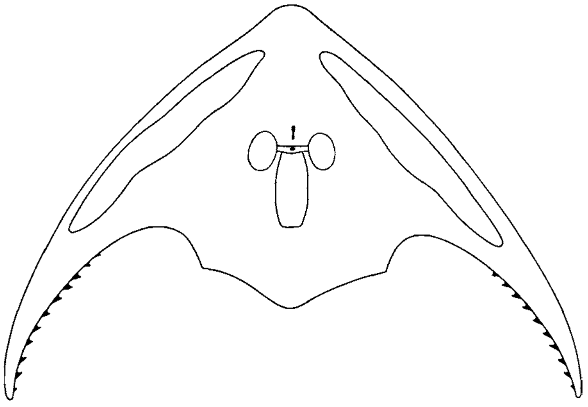


Fig. 29. — *Cephalaspis deltoides* n. sp. Restoration of the cephalic shield in dorsal view. After the holotype (ENS no. 494). Nat. size.

portion to the size of the shield and roundedly oval in shape, are situated about midway on the shield and somewhat nearer to the pectoral sinus than to the anterior or posterior ends of the shield. The inter-orbital breadth is about as great as the transverse diameter of an orbital opening. The antorbital prominence is rather insignificant. An independent pineal plate was present in the living animal. The posterior division of the naso-hypophyseal opening lies on a comparatively high elevation, and the anterior division on the floor of the narrow and apparently rather deep anterior part of the circum-nasal fossa.

The exoskeleton is not well exposed for investigation and several details of its minute structure are obscure. The ornamentation of the outer face of the exoskeleton consists of numerous very small tubercles and is thus developed in about the same way as in *C. divaricata.* The superficial layer is discontinuous in the major parts of the shield and persists only in the tubercles. The middle layer has well developed radiating canals disposed in rather distinct vascular areas; the average diameter of such an area is 1.7 mm. The basal layer contains no ringsinus but in some places irregularly formed widened canals. The mucous canal system was not enclosed in the exoskeleton; there are no traces of any large circum-areal grooves and it thus seems probable that the mucous canal system was developed as a network, lodged in the grooves between the small tubercles.

Of the grooves of the sensory line system only parts of those of the main lateral line and of the infraorbital line are observed (pl. 5:1).

The endoskeleton seems to be rather well ossified but almost nothing of it is exposed in the holotype, the superficial canals being in the main parts concealed beneath the basal layer of the exoskeleton. If this layer is made transparent by means of e. g. xylol, some of the canals are indistinctly seen; it is thus eveident that the nerve canals for the lateral sensory fields are disposed as normally in the genus, and it is also seen that the canals vls_3 and vls_4 join each other in the postero-dorso-lateral corner of the orbit.

Remarks. — *Cephalaspis deltoides* is characterized by the broad triangular shape of the cephalic shield, by the very long and slender cornua with their peculiar denticulation, and by the very short rostral process. It is similar to *C. divaricata* and the two species are probably related; it differs from that species in the general shape of the shield and particularly in the shape of the cornua. *C. deltoides* reminds furthermore remotely of *C. woodwardi* (Stensiö 1932, p. 140) but the development of the inter-zonal part is quite dissimilar in the two species which are probably only distantly related. It is also similar to *Ectinaspis heintzi* (p. 443) but, apart from the differences in the first nerve canal for the lateral sensory field and the shape of this field, it diverges from this species in many respects (e. g. in the rostral part of the shield, the inter-zonal part and the cornua). About the possible relation between *C. deltoides* and *C. apicalis,* see p. 423.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Anglaspis horizon.

Localities. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, [S. W. part], in the Anglaspis horizon (no. 494). W. side of Liefde Bay: Mt Pteraspis (no. 495).

Both specimens were collected during the ENS expedition in 1939.

8. *Cephalaspis divaricata* n. sp.

(Fig. 30; pl. 6.)

Diagnosis. — A *Cephalaspis* species of rather small size with maximum breadth of cephalic shield about one and two-third times as great as length of shield in median line. Rostral margin narrow, convex, without rostral angle. Lateral margins very slightly curved. Cornua very long and slender, projecting in postero-lateral direction and reaching backwards rather far behind posterior end of inter-zonal part. Length of cornua contained about twice in distance of their tips from rostral end of shield. Inner margins of cornua with rather stout, antero-medially directed denticles. Pectoral sinus of moderate breadth, fairly deep. Inter-zonal part rather long; its breadth constituting about one-third of maximum breadth of shield. Posterior angle of inter-zonal part protracted for some distance behind postero-lateral angles. Inter-zonal part with low dorsal median ridge. Dorsal sensory field about three times as long as broad. Lateral sensory fields rather broad, extending backwards to basal parts of cornua. Orbital openings rather large, situated somewhat nearer to rostral than to posterior end of shield. Independent pineal plate present. Superficial layer of exoskeleton

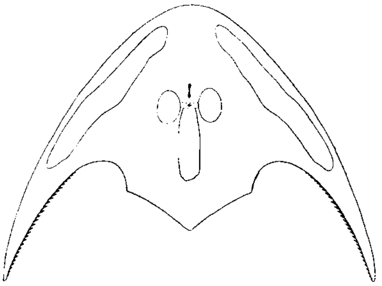


Fig. 30. — *Cephalaspis divaricata* n. sp. Restoration of the cephalic shield in dorsal view; mainly after the holotype (Pal. Mus. Oslo no. A30032). About nat. size.

discontinuous. Ornamentation consisting of very small tubercles of about equal sizes. Mucous canal system not enclosed in exoskeleton.

Holotype. — Cephalic shield (no. A30032) in the Palaeontological Museum, Oslo.

Material. — The material, which can be placed in this species with a fair degree of certainty, consists of three specimens (Pal. Mus. Oslo nos. A30032—A30034). They are all represented by more or less fragmentary cephalic shields only. The holotype (no. A30032; pl. 6) consists of a shield in counterpart, lacking the major part of the right side and the tip of the left cornu, no. A30033 mainly of the right half of a shield with the rostral end rather incomplete, and no. A30034 of the incomplete left half of a shield, wanting a considerable portion of the rostral and of the posterior parts, it is also somewhat compressed laterally. In addition to these specimens, I place here with some hesitation two very fragmentary specimens (ENS nos. 496 and Pal. Mus. Oslo no. A30035).

Description. — The holotype shield has the following dimensions. The length in the median line is 33.3 mm; the maximum breadth is estimated at 52 mm, the breadth of the inter-zonal part at 16.5 mm, and the distance of the tips of the cornua from the rostral end of the shield at about 45 mm; the distance of the pineal fissure from the rostral end of the shield is 15 mm; the height at the posterior end of the inter-zonal part is about 9 mm. The specimens nos. A30033 and A30034 are of a somewhat smaller size than the holotype; the length of the shield in no. A30033 is estimated at about 28 mm and its maximum breadth at 45 mm. No. A30035 seems to have attained about the same size as the holotype. The species was thus of fairly small size.

On account of the long and almost straight postero-laterally directed cornua the general shape of the cephalic shield is like that of an equilateral triangle, the breadth between the tips of the cornua (which is also the maximum breadth) being only slightly greater than the distance of the tips of the cornua from the rostral end of the shield.

The length of the shield in the median line constitutes about three-fifths of the maximum breadth.

The rostral margin is rather narrowly rounded but without any rostral angle. The shield is rapidly decreasing in breadth forwards. The lateral margins are only slightly curved and there are no angles nor any concavities in the margins at their transition into the rostral margin. The lateral margins of the main shield continue backwards, without any interruption, into the lateral margins of the cornua. The cornua are thus projecting in a postero-lateral direction; they are very long and slender, and reach backwards for some distance behind the posterior end of the inter-zonal part; their length constitutes about half the distance of their tips from the rostral end of the shield. The inner borders of the cornua are provided with rather stout but not very long, slightly pointed denticles, which are bent antero-medially. The pectoral sinus are rather deep but only moderately broad; they are often not uniformly concave but provided with a more or less pronounced antero-median corner. The inter-zonal part is rather long, its breadth between the postero-lateral angles is contained about three times in the maximum breadth of the shield. The posterior margin of the inter-zonal part forms a median posterior angle, which is protracted backwards to a point somewhat behind the postero-lateral angles; the margins between the posterior and the postero-lateral angles are even and almost straight. Dorsally the inter-zonal part is provided with a low, rather sharp-edged median ridge, which is slightly raised posteriorly but which does not form any crest or spine. The sensory fields are well developed. The dorsal field is elongate, about three times as long as broad; it is of about uniform breadth or very slightly tapering towards the anterior margin, which lies immediately behind the pineal groove; in the holotype the posterior margin of the field is on the whole broadly rounded, its distance from the posterior end of the shield constitutes about two-thirds of the length of the field. The lateral fields are rather broad and comparatively short, reaching backwards only over the basal parts of the cornua; they are shorter in the holotype (fig. 30) than in the other specimens. In about the middle of their length the fields are very slightly sigmoidally bent. The distance between the antero-median borders of the two lateral fields is about twice as great as the inter-orbital breadth. The orbital openings, which are rather large in proportion to the size of the shield, are roundedly oval in shape and are situated slightly in front of the middle of the length of the shield in the median line, and their distance from the pectoral sinus is somewhat less than that from the rostral end. They lie rather near to each other and the inter-orbital breadth is much less than the transverse diameter of an orbital opening. A pineal fissure indicates the presence in the living animal of an independent pineal plate.

The exoskeleton is not well exposed for observation, and could in the main only be studied from the inner side. The superficial layer is discontinuous and present only in the very small tubercles which constitute the ornamentation of the outer face of the exoskeleton. These tubercles are all of about equal size and rather closely set; along the rostral margin they are somewhat larger and flattened, and separated from each other by very narrow intervals. The middle layer has well developed radiating canals, which are disposed in distinct fascicles. The vascular areas in the middle parts of the shield are comparatively very large in the holotype, the average diameter of them being 2 mm; in no. A30033 they measure about 1.4 mm in diameter. The basal layer contains no regular ringsinus. In the posterior parts of the shield the descending vascular canals are well developed. Seen from the inner side of the exoskeleton, the descending canals open as closely set pores, and the joint pores seem to form grooves, indicating the boundaries between the vascular areas. There are often small horizontal canals connecting the descending canals and fragments of ring-shaped canals are thus formed. The mucous canal system was not enclosed in the exoskeleton; it was very probably located in open grooves between the minute tubercles and thus formed a rather uniform network.

The endoskeleton seems to have been rather poorly ossified in the holotype with the exception of its outer parts; the canals of superficial nerves and vessels are thus lined with thin perichondrial bone-layers. Also in the other specimens several of the superficial canals are very clearly exposed. The nerve canals for the lateral sensory fields are disposed as normally in the genus. The canals vls_3 and vls_4 join before they open through a common trunk into the postero-dorso-lateral corner of the orbit; the canals vls_5 and vls_6 likewise join into a common trunk, which, before opening into the canal *vcl,* receives a small vein canal, running between the canals vls_4 and vls_5.

Remarks. — *Cephalaspis divaricata* is characterized by the general, triangular shape of its shield and the long and slender postero-laterally directed cornua. It is somewhat suggestive of *C. whitei* (as represented by the holotype, cf. Stensiö 1932, fig. 30A; pl. 20:2) but differs from that species in many respects, i. a. in the size of the shield, and in the shape of the cornua and the inter-zonal part. Among the Spitsbergen *Cephalaspis* species, *C. divaricata* is very similar to *C. oreas* (p. 278) but has a larger cephalic shield than this species, and the anterior part of the shield is narrower, the shape of the inter-zonal part is different as is also the development of the exoskeleton. In general shape its shield resembles to some extent that of *C. deltoides* (p. 271), but is narrower and differs furthermore i. a. in the shape of the rostral and the inter-zonal parts of the shield, and in the more posteriorly directed cornua.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the Primaeva and ?Anglaspis horizons.

Localities. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Primaeva horizon (nos. A30032—A30034). Of the two specimens, hestitatingly placed here, one (no. 496) comes from the Primaeva horizon, the other (no. A30035) from the Anglaspis horizon.

The specimens nos. A30032—A30035 were collected during Th. Vogt's expedition in 1928 and no. 496 during the ENS expedition in 1939.

9. *Cephalaspis oreas* n. sp.

(Fig. 31; pl. 8:2).

Diagnosis. — A *Cephalaspis* species of small size with maximum breadth of cephalic shield (probably) about one and a half time as great as length of shield in median line. Shield strongly narrowing towards rostral end. Rostral margin sharply rounded without any distinct rostral angle. Lateral margins slightly convex. Cornua rather stout, projecting in postero-lateral direction (actual length of cornua unknown). Inner margin of cornua with small denticles. Pectoral sinus rather broad. Inter-zonal part comparatively narrow, with a rather low, dorso-posteriorly protracted dorsal spine. Posterior angle (at basis of dorsal spine) projecting backwards behind postero-lateral angles. Dorsal sensory field narrowly oval, about three times as long as broad. Lateral sensory fields rather broad, reaching backwards over basal parts of cornua. Orbital openings situated somewhat in front of middle of length of shield in median line. Independent pineal plate present. Exoskeleton without ornamentation. Superficial layer continuous. Mucous canal system enclosed in exoskeleton, forming a fine-meshed plexus.

Holotype. — Cephalic shield (no. A30036) in the Palaeontological Museum, Oslo.

Material. — The material referable with certainty to this species consists of the holotype (Pal. Mus. Oslo no. A30036; pl. 8:2) only; it is a rather completely preserved cephalic shield in counterpart, lacking the distal parts of the cornua. A second specimen (Pal. Mus. Oslo no. A30037), which consists of an imperfect cephalic shield, distorted by pressure of the rock, is placed here with some hesitation. Three very fragmentary shields (Pal. Mus. Oslo nos. A30038—A30039 and ENS no. 497) may belong to this species but on account of their imperfect state of preservation, which prevents a safe specific determination, they are placed here with much doubt.

Description. — The following description is based solely on the holotype. The length of the cephalic shield from the rostral end

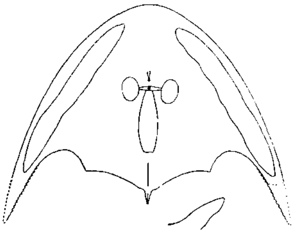


Fig. 31. — *Cephalaspis oreas* n. sp. Restoration of the cephalic shield, dorsal view; *below:* dorsal spine in lateral view. After the holotype (Pal. Mus. Oslo no. A30036). Nat. size.

to the tip of the dorsal spine is 26 mm, the breadth between the distal ends of the preserved parts of the cornua is 33.5 mm, the breadth of the inter-zonal part posteriorly is 16 mm, the height of the shield at its posterior end (the dorsal spine not included) is 7.5 mm, the distance of the pineal depression from the rostral end of the shield is 11 mm, and that of a postero-lateral angle from the rostral end is about 22.5 mm. The species was thus of small size.

The cephalic shield rapidly decreases in breadth anteriorly. Its maximum breadth, which presumably lay between the tips of the cornua, cannot be measured as the posterior parts of the cornua are missing, but is seems probable that it was about one and a half times as great as the length of the shield in the median line. The rostral margin of the shield is sharply and evenly rounded and there is no indication of a rostral angle. The lateral margins are only slightly rounded. Of the cornua only the basal parts are preserved; they seem, however, to be rather strongly built; they are rather much flattened dorso-ventrally in their most proximal parts but are posteriorly more roundedly oval in cross-section. They project in a postero-lateral direction and it seems likely that they were rather straight. They reached backwards at least to some distance behind the posterior end of the inter-zonal part. The inner margins of the cornua are provided with numerous small, slightly anteriorly curved denticles. The pectoral sinus are broad but not particularly deep. The inter-zonal part is moderately long and high and rather narrow; its breadth between the postero-lateral angles is contained about one and a half times in the length of the shield in the median line. The dorso-posterior portion of the inter-zonal part (the dorsal spine not included) is protracted somewhat backwards and the obtuse posterior angle lies behind the level of the postero-lateral angles. Dorsally the inter-zonal part is provided with a comparatively low, dorso-posteriorly protracted, bluntly acuminated median spine. The dorsal sensory field is narrow, about three times as long as broad, and oval in shape; the anterior margin is narrow, and lies immediately behind the pineal groove; the posterior margin is somewhat broader and truncated. The distance of the posterior margin of the field from the posterior end of the inter-zonal part (dorsal spine not included) is somewhat more than half the length of the field. The lateral sensory fields, which are comparatively broad, extend backwards over the basal parts of the cornua; their posterior third is placed somewhat nearer to the lateral margin than their anterior part. The distance between the antero-median ends of the two fields is about twice as great as the inter-orbital breadth. The orbital openings, which are moderately large and roundedly oval in shape, are situated slightly in front of the middle of the length of the shield in the median line. The circum-orbital rim is very narrow and inconsiderable. The pineal groove indicates that there was developed an independent pineal plate which is, however, not preserved. The naso-hypophyseal opening and the fossa circum-nasalis are not accessible to observation.

The exoskeleton is smooth without tuberculation, only very slightly rugose from the margins of the very closely placed small pores of the mucous canal system. The three layers in the exoskeleton are all well developed; the superficial layer is continuous, the middle layer has well developed vascular canals, in the main parts of the shield disposed as radiating canals, in the lateral parts placed parallel to the margins; the basal layer contains no ringsinus. The vascular areas are not very well separated from each other; in the middle parts of the shield they measure on the average 1 mm in diameter. The mucous canal system is enclosed in the exoskeleton and forms a uniformly fine-meshed network where no circum-areal and intra-areal canals can be distinguished.

Of the sensory line system only the grooves of the anterior division of the intra-orbital line have been observed between the antero-median margins of the lateral fields.

The endoskeleton is strongly ossified and comparatively well preserved, and many of the internal features of the shield are displayed. The canal sel_1 divides just antero-laterally to the orbit as is generally the case in the genus. The canals vls_3 and vls_4 join into a common trunk *(vla)* at a point immediately postero-laterally to the orbital opening. Also the canals vls_5 and vls_6 join into a rather long common trunk, which opens into the canal *vcl.*

Remarks. — *Cephalaspis oreas* is not readily characterized and distinguished from its congeners. It is extremely similar to *C. heintzi* (p. 281) and may eventually turn out to be only an aberrant form of this species, which is rather variable. With our present knowledge *C. oreas* seems to differ from *C. heintzi* in the broader and lower cephalic shield, in the cornua, which project in a more lateral direction, and which very probably are longer and slenderer, in the lower inter-zonal part, provided with a distinct dorsal spine, and in the shape of the dorsal sensory field. Fragmentary shields of the two species can often not be distinguished. From *C. divaricata* (p. 274), which is a considerably larger species, it is distinguished i. a. by the slenderer and more feebly denticulated cornua, by the larger and differently developed inter-zonal part, and by the longer lateral sensory fields. From *C. whitei* (Stensiö 1932, p. 93), which is about twice as great as *C. oreas,* it differs mainly by the broader inter-zonal part, which is provided with a real spine (in *C. whitei* there is merely a dorsal ridge), by the more anteriorly situated orbital openings and the shape of the dorsal sensory field. It seems very likely that *C. oreas* in reality is more closely related to the above mentioned *C. heintzi, C. divaricata,* and *C. whitei* than to any other known species of the genus (cf. also *C. pygmæa,* p. 285).

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the Primaeva horizon, ? the Polaris horizon.

Localities. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Primaeva horizon (no. A30036). The four specimens, more or less doubtfully placed here, come from about the same locality, nos. 497, A30037—A30038 from the Primaeva horizon, no. A30039 from a horizon 250 m above sea-level and thus from the Polaris horizon (see Kiær & Heintz 1935, p. 13).

No. A30039 was collected by Th. Vogt's expedition in 1925, nos. A30036—A30038 by Th. Vogt's expedition in 1928, and no. 497 by the ENS expedition in 1939.

10. *Cephalaspis heintzi* Stensiö.

(Fig. 32; pl. 5:3.)

1927. *Cephalaspis heintzii* in part, Stensiö, p. 270; fig. 67; pl. 36:2-3 (not pls. 29—30; 31:3; 35:1-2; 36:1).

Diagnosis. — A small *Cephalaspis* species with maximum breadth of cephalic shield about one and a half times as great as length of shield in median line. Shield strongly narrowing anteriorly. Rostral margin sharply rounded or with obtuse rostral angle. Lateral margins curved. Cornua rather long and stout, projecting in posterior, or posterior and slightly lateral, direction; reaching backwards rather far behind posterior end of inter-zonal part. Inner margins of cornua with small denticles. Pectoral sinus rather deep and narrow. Inter-zonal part comparatively narrow and high; posterior angle reaching backwards only slightly behind postero-lateral angles; dorsally provided with a low median ridge. Dorsal sensory field about twice as long as broad with broad truncated posterior margin; lateral sensory fields reaching backwards to basal parts of cornua. Orbital openings large, situated well before middle of length of cephalic shield in median line. Independent pineal plate present. Endoskeleton with very minute tubercles. Superficial layer continuous. Mucous canal system enclosed in exoskeleton, forming a fine-meshed plexus.

Holotype. — Cephalic shield (no. 59) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 270).

Material. — The material, now available, which can be referred to this species with a fair degree of certainty, consists of four specimens (ENS nos. 498—501). Nos. 498—499 are represented by somewhat imperfectly preserved cephalic shields, no. 498 (pl. 5:3) is lacking a dorso-posterior portion of the inter-zonal part, no. 499 a similar portion and the distal parts of the cornua. No. 500 consists of a shield wanting most parts of the cornua. All these specimens (nos. 498—500) seem to be somewhat affected by pressure of the rock. No. 501 consists mainly of parts of the dorsal exoskeleton of the shield, exposed in ventral view. A somewhat imperfectly preserved shield (ENS no. 502), apparently flattened by pressure of the rock, is placed here with some hesitation. — I have also had the opportunity to study the holotype.

Description. — Although this species has been described earlier by Stensiö, I shall give here an emended description as I have a rather homogenous material at hand and as I interpret the species in a more restricted sense than Stensiö. The dimensions (in mm) of the shields are given in the table below (figures in brackets are approximate). For comparison I also include here the holotype (no. 59).

Nos.	59	498	499	500	501	502
Length in median line	21.5	(22.5)	(25)	25	23	24.5
Maximum breadth	32	29	(33)	33	(28)	32
Breadth of inter-zonal part, posteriorly	15	15	(19)	16	(15)	(17)
Height of inter-zonal part, posteriorly	(8)	(10)	(10)	(12	—	—
Distance of tip of cornu from rostral end of shield	(28.5)	29.5	—	—	—	29
Distance of pineal groove from rostral end of shield	10	11	14.3	12	10	—
Distance of postero-lateral angles of inter-zonal part from rostral end of shield	20	21	25	23	21.5	20

The cephalic shield is broad, its maximum breadth, which lies across the middle parts of the cornua is distinctly, about one and a half times, greater than the length of the shield in the median line in the holotype but in other specimens not more than about one and a quarter times as great as this length. The maximum breadth is about equal to or somewhat greater than the distance of the cornual tips from the rostral end of the shield. The shield rapidly decreases in breadth forwards and the rostral margin is very narrow, sharply rounded or forming a roundedly obtuse rostral angle. The lateral margins are rather well curved. The cornua, which project in a posterior, or posterior and very sligthly lateral direction are well developed; they are rather broad and dorso-ventrally

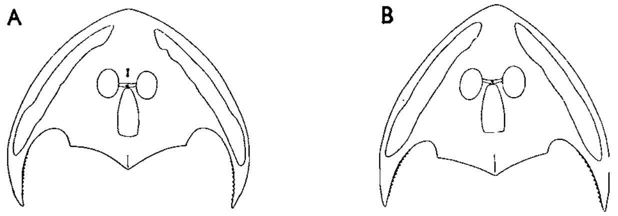


Fig. 32. — *Cephalaspis heintzi* Stensiö. Restorations of the cephalic shield in dorsal view, A, based on the holotype (Pal. Mus. Oslo no. 59), B, based on ENS nos. 498 and, partly, 500. Nat. size.

flattened; they reach far behind the posterior end of the inter-zonal part, and their length is contained about two and a half times in the distance of their tips from the rostral end of the shield. The outer margins of the cornua are rather strongly curved, more strongly than the inner margins; these latter are provided with small, slightly antero-medially curved, denticles. The pectoral sinus are rather narrow and moderately deep. The inter-zonal part is short and comparatively narrow; its breadth between the postero-lateral angles constitutes less than half of the maximum breadth of the shield. Dorsally the inter-zonal part is provided with a very low median ridge, which extends from about midway between the posterior margin of the dorsal sensory field and the posterior end of the inter-zonal part and runs backwards to the posterior angle. A dorsal spine such as indicated in Stensiö 1927, fig. 67C is, however, not developed. The dorsal sensory field is rather short and broad, not quite twice as long as broad, with the greatest breadth in the posterior half of the field; from the middle of its length it tapers forward and the anterior margin is fairly narrow, bluntly rounded; the posterior margin of the field is abruptly truncated. The distance of the posterior margin of the field from the posterior angle of the shield constitutes about two-thirds of the length of the field (the holotype) or is only somewhat less than this length (nos. 499—501). The lateral sensory fields are also rather broad; they reach backwards to about the middle of the length of the cornua or, in the holotype, slightly farther. The orbital openings are comparatively very large; they are oval or roundedly oval in shape, and situated somewhat nearer to the anterior than to the posterior end of the shield. The inter-orbital space is narrow, and its breadth is contained about one and a half times in the transverse diameter of an orbital opening. The circum-orbital rim is very narrow. The antorbital prominences are small but rather well defined. An independent pineal plate was present but is not preserved. The circumnasal fossa is rather deep anteriorly, but the nasal opening proper lies on a high elevation.

The exoskeleton is in general badly preserved. Its outer face is partly exposed in no. 498; here it is on the whole smooth, only ornamented with some scattered, irregularly placed, extremely small, often elongated tubercles (one of the largest tubercles measures 0.07 mm in length), which on the circum-orbital rim are somewhat larger and more rounded. The superficial layer, as observed in the holotype and in no. 498, forms a continuous covering to the exoskeleton. The middle layer has vascular areas with very delicate radiating canals; the diameter of a vascular area was measured to 1.4 mm in no. 501. In the posterior portion of the inter-zonal part the basal layer is well developed; it has no ringsinus. The mucous canal system is enclosed in the exoskeleton and forms a very fine-meshed network.

The endoskeleton seems to be rather well ossified but apart from canals of superficial vessels and nerves it is in general not exposed to observation. The first nerve canal for the lateral sensory field divides just antero-laterally to the orbit. The canal vls_3 opens into the dorso-lateral part of the orbit and the canal vls_4 into its dorso-postero-lateral corner, but the courses of the other canals for the dorso-lateral superficial veins could not be ascertained.

Only some parts of the grooves of the sensory line system have been observed; they offer no special interest.

Remarks. — *Cephalaspis heintzi* is characterized by its rather broad, anteriorly narrowing shield generally with a blunt rostral angle, by the broad posteriorly directed cornua, the shape of the inter-zonal part and of the dorsal sensory field. It can most likely be confused with *C. oreas* (p. 278) which occurs in the same layer, and fragmentary shields of the two species are often quite inseparable; it differs from this species in the general presence of a rostral angle, in the more posteriorly directed (probably shorter) cornua, in the absence of a dorsal spine and in the broader and differently shaped dorsal sensory field. The species is also somewhat suggestive of *C. pygmaea,* differing from it i. a. in the larger size, in the general shape and proportions of the shield, and the development of the inter-zonal part (cf. also *C. ahcticus,* p. 342).

In establishing the species *C. heintzi,* Stensiö (1927, p. 270) placed in it two specimens (Pal. Mus. Oslo nos. 53 and 54) besides the holotype, and with some doubt, also a third specimen (no. 68). With the narrower delimitation of the species used here, it seems evident that none of these specimens can pertain to *C. heintzi*. The specimens nos. 53 and 54 are in reality *C. platycephalus,* described below (p. 327), as a new species, while no. 68 is a *Cephalaspis* but indeterminable as to species.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the Primaeva horizon and the Anglaspis horizon.

Locality. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Primaeva horizon.

All specimens were collected by the ENS expedition in 1939.

The holotype is from the Fraenkel Ridge, "Horis. 200 m." and thus from the Anglaspis horizon (cf. Kiær & Heintz 1935, p. 13).

11. *Cephalaspis pygmaea* n. sp.

(Fig. 33A; pl. 9:1-3.)

Diagnosis. — A very small *Cephalaspis* species with maximum breadth of cephalic shield about one and a third times as great as length of shield in median line. Shield narrowing moderately anteriorly, rostral margin well rounded without rostral angle. Cornua rather broad and moderately long, projecting in posterior and slightly lateral direction and not reaching behind posterior end of inter-zonal part; length of cornua constitutes about one-third of distance of their tips from rostral end of shield; inner margins with small denticles. Pectoral sinus broad and shallow. Inter-zonal part short and broad, its breadth about half as great as maximum breadth of shield; posterior end protracted backwards and provided with a low median spine. Dorsal sensory field about twice as long as broad; lateral sensory fields narrow, reaching backwards to basal parts of cornua. Orbital openings situated before middle of length of shield in median line. Independent pineal plate present. Exoskeleton ornamented with numerous small tubercles. Mucous canal system enclosed in exoskeleton, forming a very fine-meshed network.

Holotype. — Cephalic shield (no. A30040) in the Palæontological Museum, Oslo.

Material. — The species is represented only by two specimens (Pal. Mus. Oslo nos. A30040—A30041). The holotype (no. A30040, pl. 9:1-2) consists of an incomplete cephalic shield, in counterpart, in which the dorsal parts of the left side are much abraded. No. A30041 (pl. 9:3) consists of the dorsal exoskeleton of the shield, exposed in ventral view; it lacks the rostral margin and the left cornu.

Description. — The holotype has the following dimensions: length in median line from rostral end to tip of dorsal spine 18.5 mm, maximum breadth 23 mm, breadth of inter-zonal part posteriorly 12 mm, height of inter-zonal part (dorsal spine not included) about 5 mm, distance of tip of cornu from rostral end of shield about 20 mm; distance of pineal fissure from posterior end of inter-zonal part about 10 mm. In no. A30041 the maximum breadth is estimated at 22 mm, the inter-zonal breadth at about 13 mm; the distance of the pineal fissure from the posterior end of the inter-zonal part is 11.8 mm. The two specimens are thus of about the same size and have belonged to a very small species.

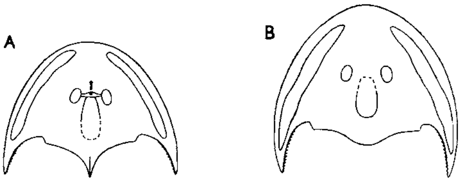


Fig. 33. — A, *Cephalaspis pygmaea* n. sp. Restoration of the cephalic shield in dorsal view. After the holotype (Pal. Mus. Oslo no. A30040). Nat. size. B, *Cephalaspis heightingtonensis* Stensiö. Attempted restoration of the cephalic shield in dorsal view. After Stensiö 1932, pl. 14:5-7. Nat. size.

The shield is rather broad; its maximum breadth, which lies between the posterior ends of the cornua, is about one and a third times as great as the median length. The shield narrows moderately towards the rostral end, but the rostral margin is still fairly broad; it is broadly curved and there is no rostral angle. The lateral margins are rather convex. The cornua project in a posterior and somewhat lateral direction and reach backwards only to the same level as the posterior end of the inter-zonal part. They are thus moderately long and their length is contained about three times in the distance between their tips and the rostral end of the shield; they are flattened dorso-ventrally and provided along their inner margins with very small denticles. The pectoral sinus are rather broad and shallow, asymmetrically developed with their greatest depth near their median borders; there is thus a well marked antero-median corner in the sinus, like that in e. g. *C. hoeli.* The inter-zonal part is short and rather broad, its breadth between the postero-lateral angles is about half as great as the maximum breadth of the shield. The posterior angle of the inter-zonal part is much protracted backwards, reaching far behind the postero-lateral angles. Dorsally there is a low median ridge beginning slightly behind the dorsal sensory field and posteriorly passing into a low, pointed, backwardly inclined, not very conspicuous dorsal spine. The dorsal sensory field is not preserved in its entire length in the holotype; in no. A30041, however, it is about twice as long as broad with its greatest breadth in the posterior half and slightly tapering towards the anterior margin which is short and truncated. The length of the field is about equal to the distance of its posterior margin from the posterior end of the dorsal spine. The lateral sensory fields are rather narrow and continue backwards only as far as to the most basal parts of the cornua. The orbital openings, which are roundedly oval in shape, are situated before the middle of the length of the shield in the median line. In the holotype the inter-orbital distance is about one and a half times as great as the transverse diameter of an orbital opening while in no. A30041 the same distance is equal to the diameter. A very narrow circum-orbital rim seems to be developed in the holotype. The antorbital prominence is not conspicuous. The presence of an independent pineal plate is indicated by the pineal fissure. The naso-hypophyseal opening is not observable but the circum-nasal fossa seems to be rather well defined though very small.

Very little of the exoskeleton is accessible to direct observation in the holotype, and in no. A30041 it is very poorly preserved. In the latter specimen the dorsal face of the exoskeleton is covered with minute tubercles, and in the holotype some tubercles are observed along the lateral margins. As to the middle layer only so much can be said that it contains radiating vascular canals. The mucous canal system is, wholly or partly, enclosed in the exoskeleton and forms a very fine-meshed network where circum-areal and intra-areal canals cannot be distinguished.

The endoskeleton is very imperfectly known. It seems to have been fairly well ossified but is poorly preserved. Only fragments of the canals of the superficial nerves and vessels are observed and there is nothing to indicate that they were disposed otherwise than in the majority of the *Cephalaspis* species.

Remarks. — Among the Spitsbergen species of *Cephalaspis, C. pygmaea* is distinguished by its very small size, the shape and proportions of the shield, especially the shape of the cornua, the pectoral sinus and the inter-zonal part. It is somewhat suggestive of *C. heintzi* (p. 281) and *C. oreas* (p. 278) but in both these species, which are of a larger size than *C. pygmaea,* the shield is more narrow anteriorly, the cornua are differently shaped, the pectoral sinus are deeper and of different form, the inter-zonal part is longer, etc., and it is thus evident that we have here to do with separate although probably closely related species. It is, however, to the British species *C. heightingtonensis* (fig. 33B; cf. Stensiö 1932, p. 96; pl. 14:5-7) that *C. pygmaea* shows a most striking similarity. Features common to the two species are the same very small size, the general shape of the cephalic shield, the shape of the cornua and the pectoral sinus, and the development of the mucous canal system. *C. pygmaea* differs from *C. heightingtonensis* by its more laterally directed cornua, the broader pectoral sinus, and in connection with this fact the narrower inter-zonal part, the shape of the posterior portion of the inter-zonal part and the presence of a dorsal spine (although it must be observed that in this respect the restoration in fig. 33B may be open to some doubt, cf. Stensiö 1932, p. 96), the shorter lateral sensory fields and the orbital openings, placed more forward. Although these differences are not very significant, they seem to prevent the two forms from being united into one species. The two species must, however, be considered to be very closely akin. The resemblance between *C. heightingtonensis* and *C. langi* is pointed out by Stensiö (1932, pp. 97, 134), and this observation applies also to *C. pygmaea* with regard to *C. langi;* the differences between these species concern the size and the shape and proportions of the shield.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the Plant horizon and the Primaeva horizon.

Localities. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Plant horizon (no. A30041), in the Primaeva horizon (no. A30040).

The two specimens were collected by Th. Vogt's expedition in 1928.

12. *Cephalaspis dissimulata* n. sp.

(Fig. 34; pls. 1:2; 8:1.)

1927. *Cephalaspis hoeli* in part, Stensiö, p. 264; fig. 64; pl. 19:2-3.

Diagnosis. — A *Cephalaspis* species of small size with maximum breadth of cephalic shield about equal to length of shield in median line. Shield more or less narrowing anteriorly, rostral margin rounded. Cornua projecting in posterior direction, reaching backwards as far as or slightly behind inter-zonal part, moderately long; their length being contained about three times in distance of tips of cornua from rostral end of shield; cornua often slightly curved medially, inner margin with rather strong, pointed denticles. Pectoral sinus narrow, with distinct antero-median corner, fairly deep. Inter-zonal part short and broad, its breadth distinctly more than half as great as maximum breadth of shield; postero-dorso-median portion protracted backwards, provided with pointed, backwardly inclined dorsal median spine. Dorsal sensory field about twice as long as broad. Lateral sensory fields extending backwards over distal half of cornua. Orbital openings situated somewhat nearer to rostral end of shield than to posterior end of inter-zonal part. Independent pineal plate present. Exoskeleton without ornamentation; superficial layer continuous. Mucous canal system generally differentiated into circum-areal and intra-areal canals.

Holotype. — Cephalic shield (no. A30042) in the Palæontological Museum, Oslo.

Material. — In the present material this species is represented by five specimens (Pal. Mus. Oslo nos. A30042—A30044, and ENS nos. 503—504). The holotype (no. A30042, pl. 8:1) consists of an almost complete cephalic shield, with the left half in counterpart. No. A30043 consists of the dorsal exoskeleton of an imperfect cephalic shield, and no. A30044 of the dorsal exoskeleton of a shield, lacking a posterior portion of the inter-zonal part; it is somewhat distorted by pressure of the rock. No. 503 is a fairly complete shield slightly affected by pressure of the rock, no. 504 is a rather imperfect shield lacking a large portion of its left side and of the inter-zonal part as

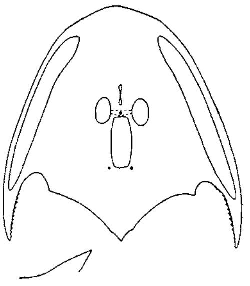


Fig. 34. — *Cephalaspis dissimulata* n. sp. Restoration of the cephalic shield, dorsal view; *below*, dorsal spine in lateral view. After the holotype (Pal. Mus. Oslo no. A30042). Nat. size.

well as the distal part of the right cornu. In addition to this material I have also studied a specimen (Pal. Mus. Oslo no. 26; pl. 1:2) referred by Stensiö (1927, p. 264) to *C. hoeli,* but now placed in this new species.

Description. — The dimensions (in mm) of the shields are given in the table below (figures in brackets are approximate):

Nos.	A30042	A30043	A30044	503	504
Length in median line	31	—	—	—	—
Maximum breadth	30.5	(34)	34	31.3	—
Breadth of inter-zonal part	18	(22)	21	18.5	(19)
Height of inter-zonal part (dorsal spine not included)	12.5	—	—	11.5	—
Distance of tip of cornu from rostral end of shield	34	—	37.5 41.3	(34)	—
Distance of a postero-lateral angle of inter-zonal part from rostral end of shield	24 25	26.5	28 30	23.5 25	27.5
Distance of pineal fissure from rostral end of shield	—	13	15	13.5	14.5

The cephalic shield is thus somewhat variable in size, but the variation lies between fairly narrow limits, and the shields must have belonged to a species of rather small size.

In general shape the shield is rather narrow and fairly high.

The shield, especially its anterior part, is somewhat variable in shape; in the holotype, and in nos. 26, 504 and A30043 this part is rather narrow, the rostral margin being narrow and fairly strongly rounded whereas in nos. 503 and A30044 the anterior part is somewhat broader and the rostral margin is more broadly rounded. The maximum breadth of the shield, which lies between the middle parts of the cornua, is about equal to the length of the shield in the median line. The rostral margin is rounded without or with a slight indication of a rostral angle; in the holotype it is somewhat asymmetrically developed, a feature which, however, is not typical for the species. The transition of the rostral into the lateral margins is marked by very obtuse antero-lateral angles or the rostral margin passes without interruption into the lateral margins; these margins are slightly convex. The cornua project in a posterior direction and extend backwards about as far as the dorsal spine of the inter-zonal part; they are moderately long and somewhat varying in length, which is contained about three times in the distance of the tips of the cornua from the rostral end of the shield. The cornua are slender, somewhat flattened and posteriorly somewhat bent in median direction; their inner margins are provided with rather large, antero-medially directed pointed denticles. The pectoral sinus are well defined but fairly narrow; they are asymmetrically developed and provided with a distinct antero-median corner, and thus the sinus have the same shape as in e. g. *C. hoeli*. The inter-zonal part, which is somewhat varying in length, is in general moderately short but with posteriorly produced dorso-median portion; its breadth is considerable, and between the postero-lateral angles amounts to distinctly more than half the maximum breadth of the shield. Dorsally the inter-zonal part is provided with a low, sharp-edged median ridge which posteriorly gradually rises to a rather short sharp-pointed spine. The dorsal sensory field is well developed, its exact shape could not be ascertained in any of the specimens placed here but very probably it is elongately oval with the anterior margin rather narrow and the posterior margin, which lies between the openings of the ductus endolymphatici, broadly rounded or truncated. The breadth of the field is about twice as great as its length. The field is bordered on each side by a ridge, which anteriorly is rather broad and depressed; posteriorly it is narrower and disappears towards the postero-lateral corners of the field. The lateral sensory fields extend over the basal parts of the cornua and reach backwards to a point at the middle of the length of the cornua; in their posterior part they decrease gently in breadth. The orbital openings which are of a moderate size and roundedly oval in shape, lie somewhat in front of the middle of the length of the shield in the median line. There is a rather low antorbital prominence. A median portion of the shield including the circum-nasal fossa and the inter-orbital space is damaged in the holotype and it is thus not possible to ascertain if there was an independent pineal plate. In the other specimens, however, a pineal fissure is clearly seen, indicating the presence of a pineal plate in the living animal. In nos. 503 and A30044 the middle division of the naso-hypophyseal opening is obliterated and there are thus separate openings for the nasal and the hypophyseal ducts. In no. A30043 there is, however, evidently a middle division; the holotype and no. 504 are imperfectly preserved in this region and therefore nothing can be said about the development of this opening.

The exoskeleton is well developed; the superficial layer is continuous and quite smooth all over the main part of the dorsal face of the shield, only along the rostral and lateral margins are there seen small, lengthened, depressed, very closely set tubercles, and in the holotype the antorbital prominence is provided with very small pointed tubercles. The middle layer has well developed radiating vascular canals. The vascular areas (and the corresponding polygonal areas, formed by the circum-areal canals of the mucous canal system) are rather variable in size. In the middle parts of the shield they are on the average 0.7 mm in diameter in the holotype and 0.9 mm in diameter in no. A30044. The mucous canal system is differentiated into wide circum-areal canals and a plexus of fine intra-areal canals in the holotype and nos. 503 and A30044; in no. A30043 on the contrary the whole mucous canal system is developed as a uniform fine-meshed plexus and this seems also to be the case in no. 504.

The endoskeleton seems to be well ossified. Only some of the superficial nerve and vascular canals are exposed. We find thus in the holotype that the nerve canal sel_1 runs undivided to the lateral field and only just medially to it gives off a strong anterior branch to the anterior part of the field, exactly as in *C. excellens*. In nos. 503 and 504 the canal seems to divide into two strong branches antero-laterally to the orbit and in no. 26 this is plainly visible (pl. 1:2), the posterior branch being somewhat narrower than the anterior one. The vein canal vls_3 opens into the postero-dorso-lateral corner of the orbit; the canals vls_5 and vls_6 join into a common canal but its proximal course, and also that of the canal vls_4, is not well exposed in the holotype, so that it is uncertain whether the common trunk and vls_4 also unite into a common canal before opening into the canal *vcl;* in no. A30043 this seems, however, to be the case.

Remarks. — *C. dissimulata* is not easily characterized and distinguished from its congeners, and this is partly due to the fact that its cephalic shield is rather variable in size and shape, and in the length of the cornua. It is generally recognized by its size, the rather narrow and high shield and the rather much backwardly protracted dorso-median portion of the inter-zonal part with its dorsal spine. *C. dissimulata* is similar to *C. hoeli* (and was originally enclosed in this species), and these two species together with *C. exilis* (p. 296) and *C. retusa* (p. 299) form a rather well defined species group within the genus. It differs from *C. hoeli* (p. 292) by the higher cephalic shield, by the slenderer and often longer cornua, by the shape the inter-zonal part and by the possession of a dorsal spine and of an independent pineal plate, and probably also by the shape of the dorsal sensory field.

As mentioned above, this species and *C. hoeli* were formerly not regarded as distinct, and of the specimens included in *C. hoeli* I now refer to *C. dissimulata* no. 26 (Pal. Mus. Oslo; Stensiö 1927, pl. 19:2 and fig. 64) on which the restoration by Stensiö of the cephalic shield of *C. hoeli* was evidently based.

Geological horizons. — Lover Eodevonian (Dittonian): Red Bay series, the Corvaspis, the Primaeva, the Polaris and the Anglaspis horizons.

Localities. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge [N. side], in the Corvaspis horizon (no. 504), in the Primaeva horizon (nos. A30042, 503) and in the Polaris horizon (nos. A30043—A30044). — No. 26 comes from a horizon "200 m. above sea-level" and this corresponds without doubt to the Anglaspis horizon (see Kiær & Heintz 1935, p. 13).

The specimens nos. A30042—A30044 were collected by Th. Vogt's expedition in 1928, nos. 503—504 by the ENS expedition in 1939.

13. *Cephalaspis hoeli* Stensiö.

(Fig. 35; pls. 10; 11:3.)

1927. *Cephalaspis hoeli* in part, Stensiö, p. 264; pls. 17—18; 19:1; 23:2; 62:1; ? pl. 68 (not pls. 19:2-3; 20—22; 23:1, 3; 24:1; 67:2).

Diagnosis. — A *Cephalaspis* species of rather small size, with maximum breadth of cephalic shield somewhat greater than length of shield in median line. Shield more or less narrowing anteriorly. Rostral margin convex, without rostral angle. Lateral margins curved. Cornua rather broad, projecting in posterior direction behind level of posterior angle of inter-zonal part, their length being contained somewhat more than three times in distance of their tips from rostral end of shield. Inner border of cornua with small forwardly curved denticles. Pectoral sinus shallow with distinct antero-median corner. Inter-zonal part of cephalic shield short and broad; its breadth being about half as great as maximum breadth of shield; dorsally provided with a low median ridge. Posterior angle of inter-zonal part extending backwards behind postero-lateral angles. Dorsal sensory field long and narrow, about three times as long as broad. Lateral sensory fields extending backwards on basal half of cornua. Orbital openings rather large, situated in about middle of length of shield in median line. No independent pineal plate. Outer face of exoskeleton smooth or ornamented with very small tubercles. Mucous canal system consisting of fine-meshed plexus.

Holotype. — Cephalic shield (no. 22) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 264).

Material. — Of the material at my disposal six specimens, Pal. Mus. Oslo nos. A30045—A30046, A30047 (pl. 11:3), A30048—A30049, A30050 (pl. 10) can be referred to this species. They all consist of more or less defect cephalic shields. Of the original material of

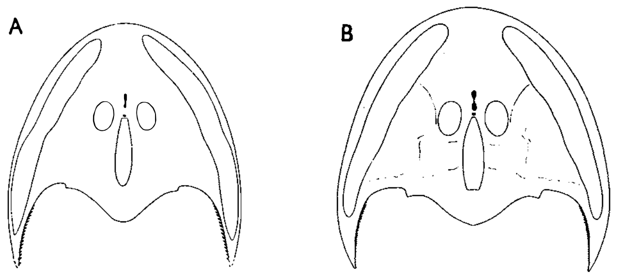


Fig. 35. — *Cephalaspis hoeli* Stensiö. Restorations of the cephalic shield; A, after the holotype (Pal. Mus. Oslo no. 22), B, mainly after Pal. Mus Oslo no. A30050. Dorsal view. Nat. size.

this species, which is rather heterogeneous, I have had on loan for a closer inspection the following specimens, belonging to the species in the restricted sense here accepted, viz. nos. 19, 22, 25, 28 (Pal. Mus. Oslo).

Description. — The dimensions of the cephalic shields (in mm) are as follows (figures in brackets are only approximate); for comparison I have also measured the holotype (no. 22):

Nos.	A30045	A30046	A30047	A30048	A30049	A30050	22
Length in median line ..	23.0	30.5	28.5	26.5	—	(28)	27
Maximum breadth	(31)	(35)	(35)	(36)	(37)	(37)	(31)
Breadth of inter-zonal part	13.8	17.4	(18)	18	18.5	17.5	15
Distance of tip of cornu from rostral end of shield	31.5	39.0	36.0	—	—	—	—
Distance of pineal foramen from rostral end of shield	11	16.3	14.8	13.9	—	—	14
Distance of pineal foramen from posterior end of shield	11.5	14.0	13.5	12.4	—	14.9	12.9

The maximum height of the shield (at the posterior end of the inter-zonal part) is only roughly estimated at 7.5 mm in no. A30046 and at 9 mm in no. A30050. The species thus seems to have attained but a rather small size.

The cephalic shield is rather variable in shape, being comparatively narrow or fairly broad, with the maximum breadth somewhat greater than the length of the shield in the median line or at most one and a third times as great as this length. The shield is more or less decreasing in breadth forwards, and the rostral margin is accordingly rather narrow or rather broad; it is also narrowly or broadly rounded, but no rostral angle is developed. The lateral margins are fairly convex. The cornua, which are rather long, broad and flattened, project in a posterior direction and reach far behind the level of the posterior angle of the inter-zonal part. Their length constitutes about one third of the distance from their tips to the rostral end of the shield. The outer margins of the cornua are rather rounded and the cornua are posteriorly somewhat curved medially so that the maximum breadth of the cephalic shield lies between the bases or the middle parts of the cornua. The inner border of the cornu is provided with a row of densely set, comparatively very small, forwardly curved denticles. The pectoral sinus are distinct but very shallow and rather broad; their antero-median corners are almost rectangular (as is also the case in *C. retusa* and *C. exilis),* while the antero-lateral corners are rounded and much less pronounced, or altogether absent. The inter-zonal part is short and broad, and its breadth between the postero-lateral angles is about half as great as the maximum breadth of the shield; the postero-dorso-median portion is protracted backwards far behind the postero-lateral angles. Dorsally the inter-zonal part has a rather distinct but low and very short median ridge. The dorsal sensory field is elongately lanceolate, about three times as long as broad; the posterior margin is short and abruptly truncated. The distance of the posterior margin of the field from the posterior end of the shield is contained about twice in the length of the field. The lateral sensory fields are rather broad anteriorly but decrease somewhat in breadth backwards; they extend posteriorly on to or somewhat over the basal half of the cornua. The distance between the antero-median borders of the two fields is rather short, being about twice as great as the inter-orbital breadth. The orbital openings are comparatively large but in regard to the size of the shield they are somewhat smaller than in *C. exilis*. They are situated about midway between the rostral margin and the posterior corner of the inter-zonal part. The inter-orbital breadth is somewhat smaller than the transverse diameter of an orbital opening. The circum-nasal fossa is narrowly triangular in shape and rather well defined. There was no independent pineal plate developed between the orbital openings (cf. fig. 4A).

The exoskeleton is very badly preserved in most of the specimens. The superficial layer forms a continuous covering to the middle layer; it is apparently smooth and without any ornamentation in all specimens except in no. A30047, where the outer face of the exoskeleton is ornamented with very small rather scattered tubercles; the superficial layer between the tubercles seems to be very thin, if really present. In the middle layer, the radiating vascular canals are well developed and form distinct vascular areas at least in no. A30046, and the average diameter of a vascular area is here 0.9 mm. The mucous canal system is enclosed in the exoskeleton and consists of a fine-meshed network, where no circum-areal and intra-areal canals can be distinguished.

The grooves of the sensory line system are well displayed in no. A30047 and also to some extent in no. A30050 (cf. fig. 35B).

The endoskeleton is well ossified in most of the specimens. The canals of superficial nerves and vessels are well displayed in no. A30050. The nerve canals of the lateral sensory fields are disposed as normally in the genus. The vein canals vls_3 and vls_4 join into a common sinus-like cavity at the postero-dorso-lateral corner of the orbit, and the canals vls_5 and vls_6 join into a common trunk which opens into the canal *vcl.* The canal vls_6 receives from behind a rather narrow canal, vls_7 coming from the zonal part of the shield.

Remarks. — *C. hoeli* forms together with *C. retusa, C. exilis* and *C. dissimulata* a small group of closely allied species. *C. hoeli* differs from *C. exilis* (p. 296) by its greater size, the general shape of the cephalic shield (the broad anterior part, the rounded lateral margins), the shape and the denticulation of the cornua, and the shape and extent backwards of the dorsal sensory field. From *C. retusa* (p. 299) it differs by the greater size and by the narrower rostral part of the shield, the somewhat slenderer cornua, and by the shape of the inter-zonal part. The differences between *C. hoeli* and *C. dissimulata* are noted under the remarks on this latter species (p. 291).

The species *C. hoeli* in the original conception of Stensiö is here thought to be a rather heterogeneous complex, and it is therefore split up into several distinct species, viz. *C. hoeli* s. str., *C. exilis, C. retusa,* and *C. dissimulata.* Of the original material of nineteen certain (Pal. Mus. Oslo nos. 18—35, 39) and seven dubious (Pal. Mus. Oslo nos. 36—42) specimens, the following will remain in the species, viz. nos. 19—20, 22—23, 25, 28, 31, 34, and 40; the specific determination of nos. 36—38 is more or less doubtful, while the following belong to other species: nos. 18, 21, 24, 26—27, 29—30, 32—33, 35, 39, 41—42.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the Ctenaspis and the Benneviaspis horizons.

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, without closer indication of locality (no. A30049); Western Plateau in the Ctenaspis horizon (nos. A30046, A30050) and in the Benneviaspis horizon (no. A30045); between the First and Second Glaciers ("Tunge"; no. A30047); the Second Glacier, in the moraine (no. A30048).

The specimens were all collected in 1928 by Th. Vogt's expedition.

14. *Cephalaspis exilis* n. sp.

(Fig. 36; pls. 11:4-5; 27:1; 34:1)

1927. *Cephalaspis hoeli* in part, Stensiö, p. 264; pls. 20—22; 23:3; 24:1; 67:2.

Diagnosis. — A *Cephalaspis* species of small size with maximum breadth of cephalic shield slightly exceeding length of shield in median line. Shield rather strongly narrowing anteriorly. Rostral margin narrow, well rounded, without rostral angle. Lateral margins feebly rounded. Cornua rather broad, fairly long, projecting in posterior and slightly lateral direction, reaching far behind posterior end of inter-zonal part; their length being contained about three times in distance of their tips from rostral end of shield. Inner margins of cornua with closely set, rather strong, hook-like denticles. Pectoral sinus rather narrow, shallow, with antero-median corner. Inter-zonal part short and broad, its breadth between postero-lateral angles about half as great as maximum breadth of cephalic shield; dorsally with low and short median ridge. Postero-dorsal portion of inter-zonal part reaching backwards behind postero-lateral angles. Dorsal sensory field long and narrow, about three times as long as broad. Lateral sensory fields extending backwards over proximal half of cornua. Orbital openings comparatively large, situated somewhat in front of middle of length of shield in median line. No independent pineal plate. Outer face of exoskeleton smooth or ornamented with minute tubercles; middle layer with large vascular areas.

Holotype. — Cephalic shield (no. A30053) in the Palaeontological Museum, Oslo.

Material. — The material of this species consists of thirteen specimens, Pal. Mus. Oslo nos. A30051, A30052 (pl. 11:4), A30053 (pl. 11:5), A30054—A30060 and ENS nos. 505 (pls. 27:1; 34:1) 506—507. Beside these specimens I have had on loan the following, which belong to the original material of *C. hoeli* (Stensiö 1927, p. 264) but which I place in this new species, viz. Pal. Mus. Oslo nos. 24, 30, 32, 41. The holotype (no. A30053) consists of a rather complete cephalic shield in counterpart. Nos. 505, 507, A30051—A30052, A30054—A30055 also consist of fairly well preserved shields, some of them are, however, slightly distorted by pressure of the rock. The remaining specimens (nos. 506, A30056—A30060) consist of fragmentary shields.

Description. — As most of these specimens consist of rather fragmentary or distorted cephalic shields, measurements could only be taken on five specimens. The dimensions of the shields (in mm) of these specimens are as follows (figures in brackets are approximate):

Fig. 36. — *Cephalaspis exilis* n. sp. Restoration of the cephalic shield; dorsal view. After the holotype (Pal. Mus. Oslo no. A30053) and Pal. Mus. Oslo no. A30055. About nat. size.

Nos.	507	A30052	A30053	A30054	A30055
Length in median line	17	(20)	17.3	17.6	19.5
Maximum breadth	—	23.5	20.8	(22)	22
Breadth of inter-zonal part	10.3	11.2	11.0	11.6	11.0
Distance of tip of cornu from rostral end of shield	21.4	—	22.0	23.3	—
Distance of pineal foramen from rostral end of shield	—	—	8.4	—	9.5
Distance of pineal foramen from posterior end of shield	—	9.6	8.8	—	9.8

The fragments of the other shields indicate that they all have about similar dimensions as the above measured specimens. The species is thus of small size.

The shape of the cephalic shield in this species is characteristic, being rather triangular owing to the narrow anterior part of the shield and the feebly curved lateral sides. The maximum breadth, which generally lies between the middle parts of the cornua, is somewhat greater than the length in the median line and somewhat less than the distance of the tips of the cornua from the rostral end of the shield. The shield narrows more or less strongly towards the rostral margin and the rostral part of the shield is thus narrow; the rostral margin is sharply rounded and without indication of any rostral angle. The lateral margins are very slightly curved. The cornua are well developed, rather broad and flattened; they project in a posterior and slightly lateral direction and reach far behind the posterior end of the inter-zonal part; their length constitutes about one-third of the distance of their tips from the rostral end of the shield. The inner margins of the cornua are provided with rather closely set, comparatively strong, anteriorly curved, hook-like denticles. In relation to the size of the shield the denticles are more strongly developed than in the allied species *C. hoeli* and *C. retusa*. The pectoral sinus are shallow and rather narrow with a distinctly pronounced antero-median corner and more rounded and very slightly marked antero-lateral corner (the pectoral sinus have thus a similar shape as in *C. hoeli* and *C. retusa).* The inter-zonal part is broad and short; its breadth between the postero-lateral angles is about half as great as the maximum breadth of the shield; dorsally it has a well marked but very short and low median ridge. The postero-dorso-median portion of the inter-zonal part is protracted backwards and reaches somewhat behind the postero-lateral angles. The dorsal sensory field is elongate, narrowing anteriorly and posteriorly with the maximum breadth slightly behind the middle of its length; its length in the median line is about three times as great as its breadth; the anterior margin is narrower than the posterior, and both are truncated. The distance of the posterior margin of the field from the posterior end of the shield equals only about one third of the length of the field. The lateral fields are broad and extend backwards over the proximal half of the cornua; in no. A30055, however, they reach farther backwards, entering the distal half of the cornua. The distance between the antero-median corners of the two fields is rather small, being about one and a half times as great as the inter-orbital breadth. The orbital openings are very large in proportion to the size of the shield, and comparatively larger than in *C. hoeli* and *C. retusa;* they have an oval shape and lie slightly anteriorly to the middle of the length of the shield; the two openings are situated rather far from each other and the inter-orbital distance is about equal to the transverse diameter of an orbital opening. There is no independent pineal plate. An antorbital prominence is not perceptible. The circum-nasal fossa is narrowly triangular in shape and well defined.

Owing to the imperfect preservation of the exoskeleton, it is difficult to get a clear picture of its minute structure. In some of the specimens (nos. 505—506, A30056—A30057, A30059) the outer face is ornamented with very small elliptic tubercles, and it seems probable that the superficial layer is developed both in the tubercles and in the inter-tubercular spaces. In the holotype (no. A30053) and in no. A30048 the outer face is apparently quite smooth, lacking all ornamentation. The mucous canal system is probably enclosed in the exoskeleton and forms (at least in the holotype and in no. A30048) a fine-meshed network, which is not differentiated into circum-areal and intra-areal canals. In the lower division of the middle layer in all specimens, in which it is sufficiently preserved to allow observation, the radiating canals are well developed and disposed in distinct bundles, forming large polygonal vascular areas. In no. A30056 the average diameter of a vascular area is 1.1 mm. Along the rostral and lateral margins of the shield the radiating canals are substituted by canals running parallelly to the margins.

The grooves for the sensory line system are well displayed in the holotype and traces of some of the grooves are also seen in nos. 506, A30056 and A30059.

The endoskeleton is well developed and displays many of the internal structures in several specimens (nos. 507, A30052—A30053, A30055, A30057, and particularly no. 505). In the holotype, in no.

A30055 and on the right side of no. A30052 the canal *vls*$_3$ opens into the postero-dorso-lateral corner of the orbit, and the canals *vls*$_4$, *vls*$_5$, and *vls*$_6$ all open into the canal *vcl;* on the left side of no. A30052 the proximal courses of the mentioned canals are much obscured owing to the development of wide superficial vein sinus.

Remarks. — *C. exilis* is very closely allied to *C. hoeli* (p. 292) and *C. retusa.* It differs from these species by the narrow anterior part of the shield, the comparatively large orbital openings, and by more strongly developed denticles on the cornua, furthermore from *C. hoeli* by the small size and by the dorsal field, reaching farther backwards, and from *C. retusa* by the somewhat differently shaped inter-zonal part (see also the remarks on this latter species, p. 301).

As far as can be seen, the following specimens in the original material of *C. hoeli* must be transferred to *C. exilis,* viz. Pal. Mus. Oslo nos. 24, 30, 32, 41, and, with some doubt, nos. 29 and 35.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the horizon A, the Ctenaspis and Benneviaspis horizons.

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, without closer indication of locality (nos. 505, A30052, A30058); W. Plateau, in the Ctenaspis horizon (nos. A30053, A30055—A30057, A30059), in the Benneviaspis horizon (nos. A30051, A30054), in the horizon R (corresponding to a part of the Benneviaspis horizon; no. A30060). W. side of Liefde Bay: the mountain S. of the Ida Glacier, N. side (nos. 506—507).

The specimens nos. A30051—A30057, A30060 were collected by Th. Vogt's expedition in 1928, nos. 505—507 by the ENS expedition in 1939.

15. *Cephalaspis retusa* n. sp.

(Fig. 37; pl. 9:4-7.)

1927. *Cephalaspis hoeli* in part, Stensiö, p. 264; (?) pl. 23:1.

Diagnosis. — A *Cephalaspis* species of small size, with maximum breadth of cephalic shield somewhat greater than length of shield in median line. Shield slightly narrowing anteriorly. Rostral margin broad, obtusely rounded. Lateral margins slightly curved. Cornua fairly broad and long; their length constituting about one-third of distance of their tips from rostral end of shield; projecting in posterior and slightly lateral direction, reaching behind posterior end of inter-zonal part. Inner margins of cornua with small denticles. Pectoral sinus rather narrow, shallow, with distinct antero-median corner. Inter-zonal part short, fairly broad; its breadth posteriorly about half as great as maximum breadth of shield; dorsally with low, short median ridge. Dorsal sensory field long and narrow. Lateral sensory fields reaching backwards to middle parts of cornua. Orbital openings of moderate size, situated midway between rostral and posterior ends of shield. No independent pineal plate. Outer face of exoskeleton smooth, without ornamentation. Mucous canal system enclosed in exoskeleton, forming fine-meshed network.

Holotype. — Cephalic shield (ENS no. 508).

Material. — The material which I refer to this species consists of the holotype (ENS no. 508, pl. 9:4), a complete cephalic shield in counterpart, and two specimens (Pal. Mus. Oslo nos. 18, 33) which constitute a part of Stensiö's material of *C. hoeli;* no. 18 (pl. 9:6-7) is a cephalic shield lacking a dorso-median portion as well as a distal part of the left cornu, no. 33 (pl. 9:5) is a nearly complete cephalic shield partly in counterpart.

Description. — The dimensions (in mm) of the shields are as follows (figures in brackets are approximate):

Nos.	508	18	33
Length in median line	20.5	(20)	(18.5)
Maximum breadth	24	23	20.7
Breadth of inter-zonal part, posteriorly	11.5	11	10.5
Distance of tip of cornu from rostral end of shield	26	—	25.5

The shields thus belong to a species of small size.

The maximum breadth of the shield, which is situated between the middle parts of the cornua, is somewhat greater than the length in the median line, being in the holotype one and a fifth times as great as this length, in the other specimens somewhat smaller. Taken as a whole the cephalic shield is less triangular than usual, only slightly decreasing in breadth towards the rostral margin. This margin is comparatively very broad, broadly (no. 18) or truncately (the holotype) rounded, so that there is no trace of a rostral angle. The lateral margins are slightly curved. The cornua project in a posterior and very slightly lateral direction, are proximally broad and flattened and taper rather rapidly towards their pointed tips; they are fairly long with a length contained about three times in the distance of their tips from the rostral end of the shield, and reach far behind the posterior end of the inter-zonal part. The outer margins of the cornua are slightly convex but the inner margins are almost straight. The inner borders of the cornua are provided with small, antero-medially directed, slightly curved denticles. The pectoral sinus are shallow and rather narrow, asymmetrically built with a distinct antero-median corner, and are thus of the same shape as in *C. hoeli* and *C. exilis*. The inter-zonal part of the shield is short, fairly broad and moderately high; its breadth constitutes about one-

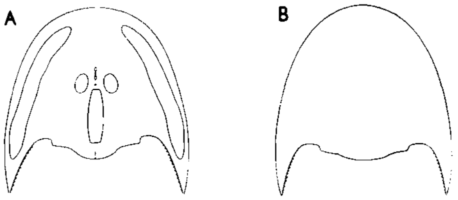


Fig. 37. — *Cephalaspis retusa* n. sp. Restorations of cephalic shields, A, after the holotype (ENS no. 508), B, outlines of the shield no. 18 (Pal. Mus. Oslo). Nat. size.

half of the maximum breadth of the shield. Dorsally the inter-zonal part is provided with a low, very short median ridge. The postero-median portion of the inter-zonal part is rather bluntly rounded, slightly protracted backwards and not reaching far behind the postero-lateral angles. The dorsal sensory field is rather narrow and about three times as long as broad; the lateral margins of the field are slightly rounded and the posterior as well as the anterior margin truncated. The posterior margin lies rather near to the posterior end of the shield, and the distance between these points is contained about three times in the length of the field. The lateral sensory fields are rather broad and reach backwards to about the middle of the length of the cornua. The orbital openings are of a moderate size and comparatively smaller than those of *C. hoeli* and *C. exilis;* they are roundedly oval in shape and situated in about the middle of the length of the shield. Very little is seen of the inter-orbital space; an independent pineal plate was not developed.

The exoskeleton is very poorly preserved. As far as could be observed there is no ornamentation on its outer face and the superficial layer seems to be continuous. Nothing is seen of the vascular canals of the middle layer. The mucous canal system (very probably) is enclosed in the exoskeleton and forms a uniformly fine-meshed network.

The endoskeleton is very poorly preserved in the holotype and in no. 33, much better in no. 18; it is evident that the ossification was rather feeble, and the bone-layers are very thin with the exception of those of the superficial canals. The nerve canal sel_1 branches just antero-laterally to the orbit and thus behaves as normally in the genus. Nothing worthy of notice is seen of the canals for the dorso-lateral superficial veins.

Remarks. — *C. retusa* was included in *C. hoeli* by Stensiö (1927, p. 264). With the narrower species concept used in this paper, *C. retusa* is treated as a distinct species. It is characterized by its small size, the broad rostral margin of the shield and the rather broad cornua. It is extremely similar to *C. exilis* and *C. hoeli* and is undoubtly very closely related to these two species and probably also to *C. dissimulata.* It differs from *C. exilis* (p. 296) and *C. hoeli* (p. 292) by the shape of its shield, only slightly narrowing anteriorly and with a very broad rostral margin, by the broader cornua and the smaller orbital openings, and from *C. hoeli* furthermore by its smaller size, by the shape of the inter-zonal part and the dorsal sensory field. It must be noted that *C. retusa* is most similar to *C. exilis*, and although the two species seem to differ rather considerably in the general shape of the shields, it must be born in mind that in other species (e. g. *C. hyperboreus, C. excellens)* this character is subject to rather great variation. Within the present material the two species seem to be fairly constant and as real intermediate forms are wanting, I think it best to regard them, at least provisionally, as distinct species.

To this species must be referred (besides the specimens mentioned above) no. 39, very probably also no. 21, and somewhat doubtfully a specimen numbered 46, all in the Palaeontological Museum, Oslo, which were placed in *C. hoeli* by Stensiö.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, horizons J, R (corresponding to parts of the Ctenaspis and the Benneviaspis horizons, respectively; cf. Kiær & Heintz 1935, p. 15—16).

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis [S.W. side], in the horizon J (no. 18), in the horizon R (no. 33), without statement of the horizon (no. 508).

Nos. 18 and 33 were collected by A. Hoel in 1909 (Stensiö 1927, p. 266), the holotype (no. 508) by the ENS Spitsbergen expedition in 1939.

16. *Cephalaspis eukeraspidoides* Stensiö.

(Fig. 38; pl. 58:3.)

1927. *Cephalaspis eukeraspidoides,* Stensiö, p. 267; fig. 65; pl. 32:1.

Diagnosis. — A *Cephalaspis* species of medium size with maximum breadth of cephalic shield about one and a half times as great as length of shield in median line. Shield rather strongly narrowing towards anterior end, with rostral angle. Lateral margins curved. Cornua very long, projecting in posterior direction, reaching far behind posterior end of inter-zonal part, length constituting somewhat more than half of distance between their tips and rostral end of shield. Inner border of cornua with small denticles. Pectoral sinus shallow. Inter-zonal part of shield fairly long, its posterior angle reaching backwards far behind its postero-lateral angles; dorsally with a long, low, median ridge. Dorsal sensory field about twice as long as broad. Orbital openings situated nearer to rostral than to posterior end of shield. Independent pineal plate present. Superficial layer of exoskeleton continuous; outer face without ornamentation.

Holotype. — Cephalic shield (no. 43) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 267).

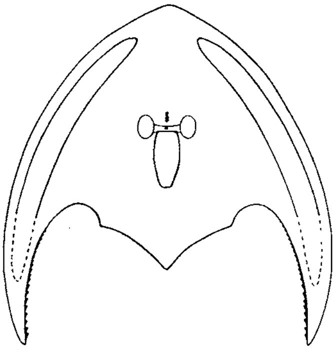


Fig. 38. — *Cephalaspis eukeraspidoides* Stensiö. Restoration of the cephalic shield, dorsal view. After the holotype (Pal. Mus. Oslo no. 43) and ENS no. 509. Nat. size.

Material. — In the new material now accumulated I can only refer one specimen (ENS 509, pl. 58:3) to this species. It consists of an imperfect cephalic shield, lacking a major part of the right side and most of the left cornu. — For comparison I had the opportunity of re-examining the holotype.

Description. — The species is described by Stensiö (1927, p. 267). Here only some remarks will be made in connection with a re-study of the holotype and an examination of the single specimen in the new material. Both specimens are imperfectly preserved and taken separately don't give a true idea of the shape of the cephalic shield. The holotype is by far the most complete specimen but its shield is posteriorly distorted and evidently rather much compressed laterally giving the inter-zonal part a much too narrow appearance. No. 509 is on the other hand somewhat depressed dorso-ventrally.

The length of the shield in the median line is 34 mm in the new specimen (no. 509) and the shield is thus only slightly smaller than that of the holotype.

The maximum breadth of the shield which lies across the middle parts of the cornua is about one and a third times as great as the length of the shield in the median line or somewhat smaller than the distance of the tip of a cornu from the rostral end of the shield and somewhat greater than the distance of the rostral end from a point midway between the tips of the cornua. The shield is much narrowing forwards and the lateral margins are fairly strongly convex. The rostral margin is narrow, and is in the holotype provided with a fairly distinct rostral angle, which is almost lacking in no. 509. The inner margins of the cornua are provided with small denticles, which anteriorly are minute and almost straight but posteriorly are somewhat larger and hook-like. The exact shape of the inter-zonal part is obscure; it is, however, evident that it was fairly narrow and that its postero-dorso-median portion is protracted backwards so that the posterior angle lies much behind the postero-lateral angles. On its dorsal side the inter-zonal part has a long and low, but fairly sharp and distinct median ridge which does not seem to be continued backwards into a dorsal spine. The dorsal sensory field is distorted in the holotype; in no. 509 it is about twice as long as broad; its anterior margin, lying immediately behind the pineal groove, is abruptly truncated, the lateral margins are only slightly curved. In both the holotype and no. 509 the distance of the posterior margin of the field from the posterior end of the interzonal part is somewhat greater than the length of the field. The pineal fissure indicates the presence of an independent pineal plate in the living animal. The naso-hypophyseal opening is comparatively small. The circum-nasal fossa is small and well defined, its anterior margin is strongly rounded.

As far as could be observed also in no. 509 the superficial layer of the exoskeleton is continuous and quite smooth, without any ornamentation. It is pierced by the rather large, closely set pores of the mucous canal system. The development of this latter system could otherwise not be observed directly but it seems probable that it formed a uniformly fine-meshed plexus.

Remarks. — It is impossible at present to make definite statements about the relationship of *C. eukeraspidoides* to other species of the genus or to point out the most kindred species. It is compared by Stensiö (1927, p. 267) with *C. hoeli,* and the species is possibly related to the group of species, represented by *C. hoeli. C. eukeraspidoides* is likewise somewhat suggestive of the new species *C. acuminata* (p. 258), *C. producta* (p. 390) and *C. oblonga* (p. 393), but, as seen from the descriptions of these species, the differences are striking and there is very probably no very close affinity between any of them and *C. eukeraspidoides.* The species is furthermore slightly similar to *C. vogti* (p. 314), *C. arcticus* (p. 342) and the British *C. lankesteri* (Stensiö 1932, p. 123) but cannot be confused with any of these species.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the horizon R (corresponding to a part of the Benneviaspis horizon).

Locality. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, in talus (no. 509).

The single new specimen was collected during the ENS expedition in 1939.

17. *Cephalaspis hyperboreus* n. sp.

(Fig. 39; pls. 12:3-4; 19:1)

Diagnosis. — A *Cephalaspis* species of medium size with maximum breadth of cephalic shield somewhat exceeding length of shield in median line. Cephalic shield more or less narrowing toward rostral end. Rostral margin strongly curved. Lateral margins slightly convex. Cornua projecting in posterior direction, somewhat curved, comparatively short, their length being contained about three and a half times in distance of their tips from rostral end of the shield; inner margins of cornua without denticles. Pectoral sinus rather narrow and shallow. Inter-zonal part short and broad, moderately high; dorsally with low median ridge; breadth of inter-zonal part greater than half of maximum breadth of shield. Dorsal sensory field rather small, less than two and a half times as long as broad. Lateral sensory fields extending backwards to basal parts of cornua. Orbital openings rather small, situated very slightly before middle of length of shield. Independent pineal plate present. Exoskeleton smooth, without ornamentation. Superficial layer continuous. Middle layer with irregularly radiating canals. Mucous canal system enclosed in exoskeleton, forming a fine-meshed plexus.

Holotype. — Cephalic shield (ENS no. 512).

Material. — The material, which I place in this species, consists of five specimens (ENS nos. 510—514). The holotype (no. 512, pl. 19:1) is represented by a rather well preserved cephalic shield, partly in counterpart, lacking only the distal part of the left cornu. Nos. 510 and 511 (pl. 12:3-4) consist of shields without parts of the cornua, no. 513 is lacking a dorso-median portion of the shield. A fragmentary shield (Pal. Mus. Oslo no. A30061) is placed here with much hesitation.

Description. — The dimensions (in mm) of the shields are as follows (figures in brackets are approximate):

Nos.	510	511	512	513	514
Length in median line	41	(42)	44	—	(40)
Maximum breadth	(46)	48	51	48	(46)
Breadth of inter-zonal part, posteriorly	—	27.5	31	30	29
Height of inter-zonal part, posteriorly	17	(16)	18	—	—
Distance of tip of cornu from rostral end of shield	45	49	52	48	—
Distance of pineal groove from rostral end of shield	21.5	21	22.5	—	22.5

The shields belong thus to a species of only moderate size.

The shield is comparatively long and narrow; its maximum breadth, which lies approximately between the middle parts of the cornua, is somewhat greater (or generally about one and a fifth times as great) than the length of the shield in median line. The shield is more or less narrowing anteriorly, more so in nos. 510—511, 514 than in nos. 512—513; the shield is thus showing the same variation in the breadth of its rostral part as in *C. excellens*. The rostral end of the shield is accordingly rather narrow or rather broad; in either case the rostral margin is strongly curved and there is no indication of any rostral angle. The lateral margins are only slightly convex. The cornua are rather short and their length is contained about three and a half times in the distance between their tips and the rostral end of the shield. The cornua project in a posterior direction and reach somewhat behind the posterior end of the inter-zonal part; they are more (no. 512) or less (no. 511) curved in a median direction and also flattened dorsoventrally. Their inner margins are not provided with denticles. The pectoral sinus are narrow and rather shallow. The inter-zonal part is short and broad, and its breadth between the postero-lateral angles is distinctly greater than half of the maximum breadth of the shield; the posterior angle, which is roundly obtuse, reaches somewhat behind the postero-lateral angles. The height of the inter-zonal part is rather moderate, being somewhat more than half as great as the breadth of the inter-zonal part posteriorly. Dorsally the inter-zonal part between the dorsal sensory field and the posterior end is raised to a low, round-edged median ridge, and this ridge is thus of about the same shape as that in *C. excellens*. The dorsal sensory field is comparatively small; it is rather narrow, and about two and a half times as long as broad, the posterior margin is more or less broad and truncated. The anterior margin of the field is rather broad and situated immediately behind the pineal fissure (no. 511), or sharply rounded and lies somewhat behind the pineal fissure (the holotype). The length of the field is always smaller than the distance of its posterior margin from the posterior end of the inter-zonal part. The lateral sensory fields are of a moderate breadth and reach backwards only over the basal parts of the cornua, not extending behind the middle of their length. The distance between the antero-median corners of the two fields is somewhat variable according to the breadth of the rostral part of the shield, being about three times as great as the inter-orbital breadth. The orbital openings are rather small, roundedly oval in shape, and situated only slightly before the middle of the length of the shield in the median line. The circum-orbital ridge is narrow; the antorbital prominence is feebly developed. The inter-orbital breadth is about twice as great as the transverse diameter of an orbital opening. A separate pineal plate was present. The naso-hypophyseal opening is normally developed; the circum-nasal fossa is triangular in shape and well defined but rather shallow.

The exoskeleton is well developed; its dorsal face is only observable

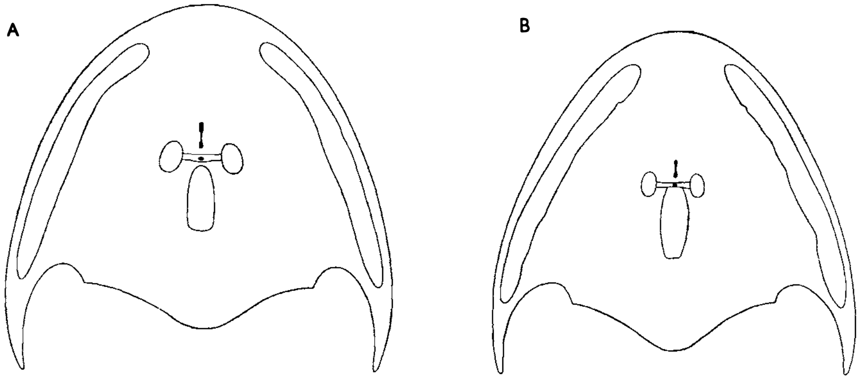


Fig. 39. — *Cephalaspis hyperboreus* n. sp. Restorations of the cephalic shield, dorsal view, A, after the holotype (ENS no. 512), B, after ENS no. 511. Nat. size.

in some places, it seems to be quite smooth without any ornamentation. In no. A30061, placed with doubt in this species, the exoskeleton is ornamented with small tubercles, of different size and shape, blunt or pointed; as the preservation of the exoskeleton is very poor in this specimen, it cannot be ascertained if the superficial layer really is continuous or not. In the other specimens this layer forms a continuous covering to the middle layer. In the middle layer the minute vascular canals are in the main disposed as radiating canals but are rather irregular and provided with many small side branches. The basal layer contains no ringsinus. The mucous canal system is enclosed in the exoskeleton and consists of a very fine-meshed network in which no circumareal and intra-areal canals can be distinguished.

With the exception of the canals for superficial nerves and vessels, the endoskeleton seems to be poorly ossified. The nerve canal sel_1 is developed as normally in the genus and branches just antero-laterally to the orbital opening. The canal vls_3 enters the postero-dorso-lateral corner of the orbit and the canals vls_4 and vls_5 join into a common trunk before opening into the canal *vcl*.

Remarks. — *C. hyperboreus* is characterized by its comparatively long cephalic shield, the rather short cornua without denticles, the shallow pectoral sinus and the shape of the broad inter-zonal part. In the general shape of its shield *C. hyperboreus* is slightly reminiscent of *C. sinuata, C. eurynotus,* and *C. dissimulata* but shows distinct differences in the above mentioned characteristics. The species is, however, similar to *C. excellens* (p. 308) and to *C. fletti* (Stensiö 1932, p. 127) from the Dittonian of England. From the latter species it differs mainly by the shorter cornua devoid of denticles, by the orbital openings placed near the middle of the length of the shield, and by the small dorsal field. From *C. excellens* it differs i. a. by the anteriorly more narrowing (triangular) shield, the shorter cornua and the absence of denticles on them, the shallow pectoral sinus, the normal development of the naso-hypophyseal opening and of the first nerve canal to the lateral sensory field. It seems rather probable that *C. hyperboreus* is related to these two species.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Primaeva horizon.

Localities. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Primaeva horizon, in the normal red sandstone (nos. 510—514). No. A30061, doubtfully placed here, is also found on the Fraenkel Ridge and in the Primaeva horizon, but in a grey sandstone.

No. A30061 was collected by Th. Vogt's expedition in 1928, the other specimens (nos. 510—514) by the ENS expedition in 1939.

18. *Cephalaspis excellens* n. sp.

(Figs. 40—41; pls. 11:1-2; 12:1-2; 13—17; 40:4-5; 65:3; 115:2-3.)

1927. *Cephalaspis vogti?,* Stensiö, p. 268; pls. 25—26 (no. 49, hesitatingly placed in this species).

Diagnosis. — A *Cephalaspis* species of medium size with narrow or rather broad cephalic shield; maximum breadth of shield always greater than length of shield in median line. Shield more or less narrowing anteriorly. Rostral margin fairly broad, rather convex, without rostral angle. Lateral margins more or less strongly curved. Cornua rather long and slender, projecting in posterior direction, curved somewhat in median direction, and reaching behind posterior end of shield; length of cornua contained about two and a half times (or somewhat more) in distance of their tips from rostral end of shield. Inner margins of cornua with rather small, curved denticles. Pectoral sinus rather deep and narrow. Inter-zonal part broad, its breadth generally half as great as maximum breadth of shield; postero-dorso-median portion protracted backwards; posterior end obtuse and rounded; dorsally with low, broad median ridge. Dorsal sensory field situated at some distance behind pineal plate, small, at most twice as long as broad, anterior and posterior margins truncated. Orbital openings situated before middle of length of shield. Independent pineal plate present. Separate openings for nasal and hypophyseal ducts. Outer face of exoskeleton in the main smooth; superficial layer continuous. Mucous canal system enclosed in exoskeleton, differentiated into circum-areal and intra-areal canals. First nerve canal to lateral sensory field running undivided to lateral field.

Holotype. — Cephalic shield (no. A30062) in the Palaeontological Museum, Oslo.

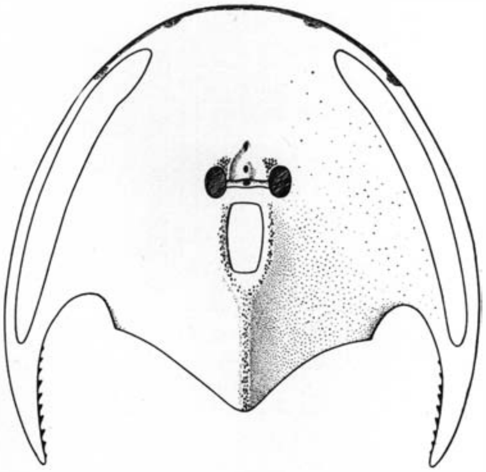


Fig. 40. — *Cephalaspis excellens* n. sp. Restoration of the cephalic shield, dorsal view; after Pal. Mus. Oslo no. A30063. × 1½.

Material. — The material of this species consists of seventeen specimens, Pal. Mus. Oslo nos. A30062 (pls. 11:2; 13—14; 15:1-2; 16:1), A30063 (pls. 12:2; 40:4-5), A30064, and ENS nos. 515 (pls. 12:1; 16:2; 17), 516—517, 518 (pl. 115:2), 519 (pl. 115:3), 520—521, 522 (pl. 15:3-4), 523 (pl. 11:1), 524—526, 527 (pl. 65:3) and 528. An additional specimen (ENS no. 529) is placed here with some hesitation. All the specimens consist of cephalic shields, some of them (nos. A30062—A30063, 515—519) are almost complete and often remarkably well preserved; the other shields are more or less fragmentary.

Description. —The dimensions of some of the shields (in mm) are given in the table below (figures in brackets are approximate):

Nos.	A30062	A30063	A30064	515	516	517	518	519
Length in median line	(35)	35.6	35	38	(37)	35.8	34	(38)
Maximum breadth . . .	47	42	(44)	43	50.5	(39)	(41)	43
Breadth of inter-zonal part between postero-lateral angles	(24)	23	(23)	22.5	27	18	22.5	(21)
Height of inter-zonal part	(10)	8.5	7.5	9	—	11.5	10	12
Distance of tips of cornua from rostral end of shield	45.5	45	44	47	—	45.9	(42)	(48)
Distance of pineal groove from rostral end of shield	16.5	16	16.5	—	(18)	16.7	15.6	(17)

As is seen from the measurements given above and also from the restorations in fig. 41 there is a considerable variation in the shape of the cephalic shields. Thus, the breadth of the shield is rather different in the various specimens, even if due regard is paid to possible distortions of the shields arisen from pressure of the rocks. The differences between the narrowest and the broadest forms are so great that, at first glance, they might be supposed to represent different species. All the specimens here considered can indeed, with regard to the breadth of their shields, be divided into two indistinctly differentiated groups, one with comparatively narrow, and one with comparatively broad shields. As there are no other differences between the two groups, they must, however, be regarded as belonging to one and the same species. The material of complete shields is too scanty to allow an analysis if the species really appeared in two different forms (the differences perhaps reflecting a sexual dimorphism) as is the case in the *Poraspis* species (see Kiær & Heintz 1935, p. 53).

Taken as a whole, the shield is of medium size, rather flattened and moderately broad with the maximum breadth, which generally lies near the bases of the cornua, always greater than the length in the median line (or, more positively, from slightly exceeding the length to about one and a third as great as the length).

The shield is more or less narrowing anteriorly, and the rostral margin is of a varying breadth but always well rounded and without any rostral angle. The rostral margin merges into the distinctly curved lateral margins without any boundary. The cornua are well developed and fairly long with a length that is contained two and a half times to three times in the distance of their tips from the rostral end of the shield. They project in a posterior direction and reach rather far behind the posterior end of the inter-zonal part. The cornua are slender and flattened dorso-ventrally, and distinctly but not very much curved inwards; their inner margins are provided with small, antero-medially directed, somewhat curved, pointed denticles. The pectoral sinus are well defined, generally rather deep and narrow, but somewhat varying in breadth; there is in some specimens an indication of an antero-median corner, but in general the sinus are uniformly concave. The inter-zonal part is fairly short but with a posteriorly protracted dorso-median portion; the posterior angle is obtuse and rounded; the posterior margin between the posterior angle and each postero-lateral angle is only very slightly concave. The inter-zonal part is comparatively broad; its breadth is varying in accordance with the breadth of the shield, and is on the average about half as great as the maximum breadth of the shield. Dorsally the inter-zonal part is provided with a broad, blunt-edged, slightly pronounced median ridge; it begins at some distance behind the dorsal sensory field and becomes gradually more distinct posteriorly. The sensory fields are fairly well developed; the dorsal field is rather small in proportion to the size of the shield; compared with that in other *Cephalaspis* species it is much shortened anteriorly as well as posteriorly. Its anterior margin lies rather far behind the pineal groove

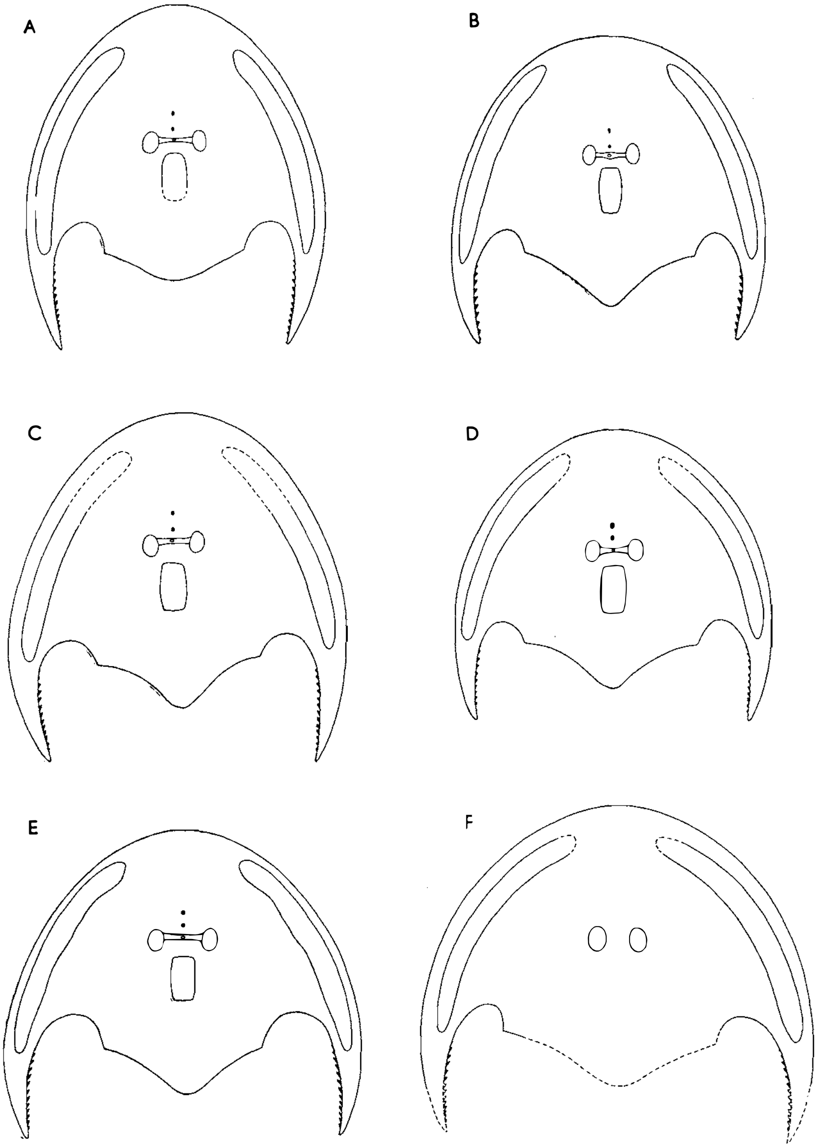


Fig. 41. — *Cephalaspis excellens* n. sp. Restorations of some cephalic shields, showing the variation in shape; A, after ENS no. 517, B, after Pal. Mus. Oslo no. A30063, C, after ENS no. 519, D, after ENS no. 518, E, after the holotype, Pal. Mus. Oslo no. A30062, F, after ENS no. 516. Nat. size.

and generally also somewhat behind the level of the posterior margin of the orbits. Posteriorly the field extends almost as far as to the openings for the ductus endolymphatici, which lie just behind the postero-lateral corners of the field. The distance of the posterior margin of the field from the posterior end of the shield is one and a half times or twice as great as the length of the field. The field is short, at most twice as long as broad, and almost rectangular in shape with rounded corners and very faintly convex margins; in nos. 517 and 527, however, the anterior margin is more distinctly rounded. On the lateral sides of the field as also, to a certain extent, anteriorly to it, there is a broad, somewhat flattened, rather indistinctly defined wall, which is more faintly pronounced posteriorly and gradually passes over into the median ridge of the interzonal part. The lateral sensory fields extend backwards over the proximal third or quarter of the cornua. The distance between their antero-median corners is about three times as great as the inter-orbital breadth. The orbital openings are placed in front of the middle of the length of the shield in the median line; they are roundedly oval in shape and bordered by a rather inconspicuous circum-orbital ridge. The interorbital distance is only somewhat greater than the transverse diameter of an orbital opening. The antorbital prominence is rather small, noticeable mainly by the coarse tuberculation. The presence in the living animal of an independent pineal plate is indicated by the pineal groove (and fissure). The nasal opening is completely separated from the opening for the hypophyseal duct by the obliteration of the middle division of the naso-hypophyseal opening. The circum-nasal fossa forms a narrow triangle and is rather shallow; the nasal opening lies on an elevation in the posterior division, and the opening for the hypophyseal duct in the anterior, somewhat deeper division of the fossa.

The exoskeleton is rather strongly developed and well preserved; its structure in the dorsal portion of the shield can thus be fairly closely studied. The superficial layer is continuous and in the main parts of the shield smooth without any ornamentation. It is pierced by the closely set pores of the mucous canal system; in some places the pore canals widen in their outer part, and the pores are thus enlarged in such a way that the superficial layer is restricted to and forms narrow sharp-edged ridges between the pores. In some places, however, the superficial layer is provided with an often feebly developed ornamentation. On the borders of the dorsal sensory field, on the median ridge of the interzonal part, along the anterior margin of the circum-nasal fossa and on the circum-orbital ridge, the ornamentation consists of very closely set, flattened tubercles of somewhat varying size and shape, often with lobate margins, separated from each other by rather narrow grooves in which open comparatively large pores of the mucous system. On the antorbital prominence the tuberculation is rather coarse (pl. 40:4). The thickened lateral borders of the shield are also tuberculated; on the cornua the lengthened tubercles of the dorsal face are more delicate than those on the lateral margin (pl. 11:1). At the transition between the lateral margins and the rostral margin there is a section with more pronounced tuberculation; antero-medially to this section, on the rostral margin, the rounded tubercles are gradually replaced by elongated ones and these, in their turn, by comparatively thick ridges, running parallelly to the margin (pl. 40:5). The margins of the ridges are crenulated, or there are small transverse walls bridging over the grooves between the ridges; in the spaces between these transverse walls open the rather wide pores of the mucous system. On each side near the rostral end of the shield, the ridges are interrupted by a batch of tubercles; between these, however, the ornamentation of the extreme rostral end of the shield consists of ridges (cf. *Aceraspis robusta,* Heintz 1939, p. 12; figs. 1—2; pl. 2:6-8). There are thus on the anterior part of the marginal rim of the shield two pairs of batches of tubercles separated by parallel ridges. The middle layer of the exoskeleton is well developed; the upper division which encloses the mucous canal system is rather thick. This system consists of comparatively wide circum-areal canals and an intra-areal mucous canal plexus (pl. 11:1). In some places one or two rows of narrow intra-areal canals have been observed (pl. 11:2) running concentrically and close to the circum-areal canals. The circum-areal and the intra-areal canals open outwards by closely set pores; in some places in the inter-zonal part of the shield the pores of the circum-areal canals have apparently partly fused with each other, forming slitlike openings to the canal, or, in other words, the canals are here represented by more or less open grooves (cf. *Hemicyclaspis murchisoni,* Stensiö 1932, pl. 9). Anteriorly on the shield, the circum-areal canals are narrow and irregularly disposed, and are entirely lacking at the rostral and lateral margins as also on the cornua. In the lower division of the middle layer the radiating vascular canals, which are of a rather fine calibre, are disposed rather uniformly, forming regular vascular areas. A very large vascular area is formed with the opening for the hypophyseal duct as its center from which the canals radiate (pl. 65:3). In other places on the shield the horizontal (submucous) vascular canals are disposed in rows or bundles, running in different directions, e. g. at an oblique angle to the rostral margin, parallelly to the lateral margins and around the orbital opening, and in a transverse direction on the dorsal side of the cornua. The size of the polygonal areas, formed by the circum-areal mucous canals and corresponding to the vascular areas, is somewhat varying, in the holotype the average diameter of a polygonal area is 0.9 mm. (Cf. also fig. 7.)

The sensory line system seems to have been lodged in very delicate grooves in the exoskeleton, and only a few of them have been observed, viz. an anterior portion of the supraorbital groove (in the circum-nasal fossa, pl. 15:2), an anterior groove for the infraorbital line (pl. 14), and a small anterior part of the groove for the main lateral line.

The endoskeleton of the cephalic shield was lined with well developed perichondrial bone-layers and in such a way well ossified. Many of the internal anatomical structures are excellently displayed (see the general anatomical part). The canal sel_1 divides just medially to the lateral sensory field in giving off a strong anterior branch to the foremost part of the field. The canal V_3 does not enter the dorsal face of the endoskeleton, it pierces the roof of the oralo-branchial chamber just antero-ventrally to the canal sel_1. The vein canal vls_3 opens either in the postero-dorso-lateral corner of the orbit or into the canal *vcl* at the transition to the orbit; in the holotype we find the first condition on the left side and the second condition on the right side of the shield (the same is met with in no. 515). The canals vls_4—vls_6 most often join into a rather long common trunk which opens into the canal *vcl* (as seen in nos. A30062, A30064, 515 and (probably) 526). In no. 522, however, the canals vls_4 and vls_5 join into a common canal which opens into the canal vls_3, and the common trunk thus formed opens into the postero-dorso-lateral corner of the orbit.

Remarks. — *C. excellens* is characterized by the shape of its shield with a somewhat varying breadth, by the short dorsal sensory field, the separate openings for the nasal and hypophyseal ducts and by the undivided canal sel_1. In external appearance it resembles rather much *C. fletti* (Stensiö 1932, p. 127) and *C. hyperboreus* (p. 305) but differs i. a. in the separate openings for the nasal and hypophyseal ducts, the short dorsal field and the shape of the cornua. It reminds also of *C. jarviki* (see this species, p. 378). *C. excellens* is, however, much more similar to, and certainly very closely related to, *C. vogti* (the following species). It differs from this species as far as known by the slightly smaller size, the more broadly rounded rostral margin and the stouter and shorter cornua.

The specimen Pal. Mus. Oslo no. 49, hesitatingly placed in *C. vogti* by Stensiö (1927, p. 268; pls. 25—26) belongs to *C. excellens;* it comes from the lowest slope of Mt Pteraspis.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Anglaspis horizon.

Locality. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge [S. side], in the Anglaspis horizon.

The specimens nos. A30062—A30064 were collected by Th. Vogt's expedition in 1928, nos. 515—529 by ENS expedition in 1939.

19. *Cephalaspis vogti* Stensiö.

(Fig. 42; pls. 12:5; 18:1.)

1927. *Cephalaspis vogti,* Stensiö, p. 268; fig. 66; pl. 27; ? pl. 31:1 (not pls. 25—26).

Diagnosis. — A *Cephalaspis* species of medium size, with maximum breadth of cephalic shield somewhat greater than length of shield in median line. Shield roundly narrowing towards rostral end. Rostral margin narrow and sharply curved, without rostral angle. Cornua long and slender, projecting in posterior direction, somewhat

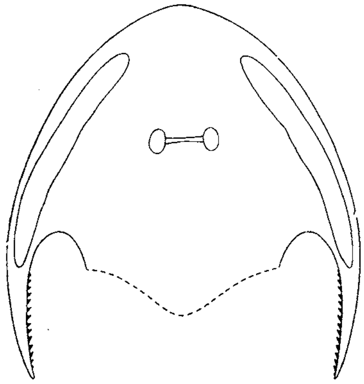


Fig. 42. — *Cephalaspis vogti* Stensiö. Partial restoration of the cephalic shield, dorsal view. After the holotype (Pal. Mus. Oslo no. 46) and Pal. Mus. Oslo no. A30065. Nat. size.

medially curved; length of cornua contained about two and a half times in distance of their tips from rostral end of shield; inner margins of cornua with curved denticles. Pectoral sinus deep and narrow. Inter-zonal part broad. Lateral sensory fields reaching bachwards to basal halves of cornua. Orbital openings situated in front of middle of length of shield. Independent pineal plate. Superficial layer of exoskeleton generally without ornamentation; continuous. Mucous canal system with circum-areal canals and grooves and intra-areal canals. First nerve canal to lateral sensory field undivided.

Holotype. — Imperfect cephalic shield (no. 46) in the Palæontological Museum, Oslo (Stensiö 1927, p. 268).

Material. — In the new material at hand I refer only one specimen (Pal. Mus. Oslo no. A30065) to this species. It consists of a portion of the right half of a cephalic shield, including the whole cornu.

Remarks. — The diagnosis given above is based on the holotype (Pal. Mus. Oslo no. 46) and the new specimen (no. A30065), now at hand. Some remarks and additions to the original description by Stensiö (1927, pp. 268—269) will be given here.

The rostral margin is very sharply rounded but there is no distinct rostral angle. The cornua, which are now known in their entire length, are long and slender, at their bases somewhat flattened dorso-ventrally but towards their tips more rounded in cross-section. Their length is about exactly the same as that, tentatively given in Stensiö's restoration; they are, however, somewhat more curved in median direction than in his figure. The cornua are thus longer and much slenderer than in the related *C. excellens*. The inter-zonal part is still very imperfectly known. The orbital openings are oval in shape. The pineal fissure indicates the presence of an independent pineal plate in the living animal. The exoskeleton is well developed; its outer face is smooth as far as can be observed; only on the lateral margins of the cornua there are small, low, flattened tubercles, which are not very well separated from each other. The superficial layer forms a continuous covering to the middle layer. This layer has well developed radiating canals. On the zonal part of the shield, just in front of the pectoral sinus, some traces of ringsinus are observed in the basal layer. The mucous canal system is developed in about the same way as in *C. excellens,* there are thus intra-areal plexus of fine canals, furthermore there are observed rather narrow circum-areal canals, which in some places are replaced by open grooves. The polygonal areas formed by the circum-areal canals or grooves, and in the middle layer represented by the vascular areas, are rather small, their average diameter in no. A30065 is 1.2 mm.

With regard to the disposition of the nerve canals in the endoskeleton it is important to note that the canal sel_1 is developed as in *C. excellens,* it thus runs undivided to just medially to the lateral sensory field, and is thus not splitting into two equal branches antero-laterally to the orbit as in most *Cephalaspis* species. This fact is observed both in the new specimen and in the holotype; the canal "sel_1" in Stensiö's plate (Stensiö 1927, pl. 27) is thus non-existent: although the disposition of the canals in this part of the shield is rather obscure, it is, however, evident that the linings of the said "canal" belong to different vascular canals. The canal V_3 is disposed as in *C. excellens.* In no. A30065 the vascular canals of the zonal part are well exposed (p. 173). The canals vls_4—vls_7 join into a common trunk which opens into the canal *vcl.*

As far as is known, *C. vogti* is characterized by the general shape of its shield with the maximum breadth lying across the bases of the cornua, the narrow rostral margin, the curved lateral margins, and by the long and slender cornua. It is apparently closely allied to *C. excellens* (p. 308) and with this species has in common the undivided canal sel_1 and the disposition of the canal V_3; it must, however, be noted that the development of the naso-hypophyseal opening and the shape of the dorsal sensory field, which are so characteristic for *C. excellens,* are as yet unknown in *C. vogti. C. vogti* differs from *C. excellens* mainly by the anteriorly more narrowing shield, the narrow rostral margin, and by the slenderer cornua.

In Stensiö's material, five specimens were hestitatingly placed in *C. vogti* (Stensiö 1927, p. 268, nos. 47—51); of these I think that no. 48 really belongs to this species, nos. 47 and 50 are too imperfectly preserved as to be definitely determined but may belong here, no. 47 is, however, somewhat suggestive of *C. sinuata;* no. 51 is not this species but may belong to *C. verruculosa;* no. 49 is *C. excellens.*

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Anglaspis horizon.

Locality. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Anglaspis horizon.

The single new specimen was collected by Th. Vogt's expedition in 1928.

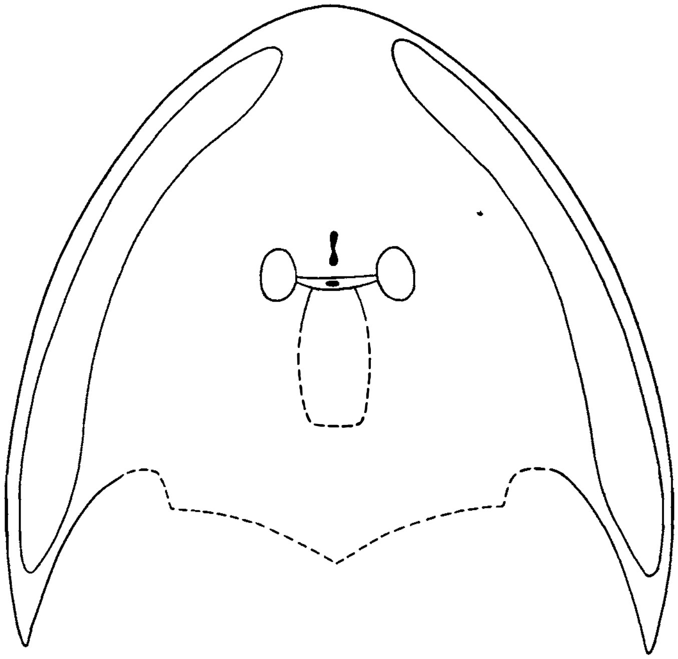


Fig. 43. — *Cephalaspis powriei* Lank. var. *polaris* n. var. Restoration of the cephalic shield in dorsal view (after ENS no. 530). Nat. size.

20. *Cephalaspis powriei* Lank. var. *polaris* n. var.

(Fig. 43; pl. 19:2.)

Diagnosis. — A variety of *Cephalaspis powriei* with cornua of cephalic shield broad and fairly long; their length being contained about three times in distance of their tips from rostral end of shield. Inter-zonal part rather narrow. Orbital openings of normal size, situated at about middle of length of shield. Dorsal sensory field broad anteriorly. Exoskeleton with delicate ornamentation; superficial layer in most places continuous. Mucous canal system generally enclosed in exoskeleton.

Holotype (for the variety). — Cephalic shield (ENS no. 530).

Material. — To the species *C. powriei* I refer as a new variety one specimen (ENS no. 530), which consists of an imperfectly preserved cephalic shield, partly in counterpart, lacking most of the left cornu and the inter-zonal part.

Description. — The maximum breadth of the cephalic shield cannot be directly measured but is estimated at maximally 95 mm; the distance of the tip of the right cornu from the rostral end of the shield is 95 mm, and the distance of the pineal fissure from the rostral end of the shield is 38 mm. The species thus attained about the same size as the Scottish specimens of *C. powriei.*

In the general shape of its shield this specimen most closely resembles the var. *asper* of *C. powriei.* The maximum breadth of the shield, which lies between the middle parts of the cornua, must have been considerably greater than the length of the shield in the median line, and is about equal to the distance of the tip of the cornu from the rostral end of the shield. The shield narrows rather rapidly towards its anterior end, the rostral part is narrow, and the rostral margin is curved without any rostral angle. The cornua are projecting in a posterior and slightly lateral direction, and of about the same general shape as in the var. *asper* but differ in being broader basally; their length constitutes about one-third of the distance of their tips from the rostral end of the shield. The middle part of the inner margin of the cornua is provided with small "denticles", which, just as in the other forms of *C. powriei,* are not comparable with the real cornual denticles in other *Cephalaspis* species, but are merely tubercles of the same kind as those constituting the general ornamentation of the exoskeleton. The shape of the inter-zonal part is unknown but it seems rather certain that this part was fairly narrow and thus more resembling that of the var. *asper* than of the var. *brevicornis* and of the typical form of *C. powriei.* The dorsal sensory field is preserved only in its anterior part, where it is rather broad and has the anterior margin truncated, thus more resembling the dorsal field of the var. *brevicornis* than of the var. *asper.* The lateral sensory fields reach backwards to about the middle of the cornua, being thus longer in this specimen than in the typical form and in the var. *brevicornis;* their exact shape in the var. *asper* is not apparent but they seem to be somewhat longer than in the other forms (cf. Stensiö 1932, pl. 30:1). The orbital openings, which are moderately small and oval in shape, seem to be situated as in the var. *asper* and thus probably at about the middle of the length of the shield, and at any rate not so far anteriorly as in the typical form or in the var. *brevicornis.* The circum-orbital ridge is rather narrow. The inter-orbital space is somewhat damaged, and the shape of the naso-hypophyseal opening and of the circum-nasal fossa could not be ascertained. The naso-hypophyseal opening seems, however, to have been rather small and, in relation to the orbits, lies not so far forwards as is the case in the var. *asper.* The pineal plate is not preserved but it must have formed a very thin bar between the orbital openings, immediately in front of the dorsal sensory field.

The exoskeleton is not easily accessible to investigation and its outer parts have been observed only in a few places. The ornamentation is of a varying development in different parts of the shield. Along the anterior and lateral margins, on the circum-orbital ridge and in some places in the middle and posterior parts of the shield it consists of numerous, very small, irregularly placed, obtuse or pointed tubercles; along the middle parts of the median margins of the cornua the tubercles are somewhat larger than in the other parts of the shield, but otherwise of the same shape. In some places in the middle part of the shield and on the dorsal side of the posterior half of the cornu the exoskeleton is quite smooth without any ornament. The superficial layer of the exoskeleton seems to be unequally developed, forming in some places a continuous covering to the middle layer, while elsewhere apparently altogether absent in the inter-tubercular spaces, and thus only present on the summits of the tubercles. The radiating vascular canals are extremely fine. No ringsinus have been observed in the basal layer. In some places, e. g. on the dorsal side of the cornu, the mucous canal system is situated entirely within the exoskeleton, in other places it seems to have been only partly enclosed in the exoskeleton or situated entirely outside of it. In one place in the middle part of the shield some rather narrow grooves have been observed; they correspond apparently to the circum-areal grooves or canals in other species, but here they are irregularly developed and often form no closed loops but only parts of a circum-areal groove. In other places the mucous canal system seems to have been developed as a uniform network of fine canals or grooves, where no distinction can be made between a circum-areal canal or an intra-areal plexus.

Of the endoskeleton only the superficial canal layers have been observed; the internal bone-layers are not ossified or have not been preserved in the fossil. The canal sel_1 is disposed as normally in the genus, thus lying closely to the lateral margin of the orbit and bifurcating just antero-laterally to the orbit. According to Stensiö (1932, pp. 40, 44, 108, 110, 114—115) the course of this canal in the Scottish forms of the species is different from that in other species, the canal is said to run rather laterally and thus not closely to the orbit and to bifurcate rather far from the antero-lateral corner of the orbit. This statement is, however, not confirmed by any of the published figures of the specimens of this species but one, viz. pl. 26:1, representing a specimen, hesitatingly placed to the var. *asper* (p. 113) or said to belong "to either *C. powriei* var. *asper* or *C. watsoni*" (explanation to pl. 26:1). It is thus impossible to get an opinion of the real and normal conditions in the Scottish forms of the species with regard to this nerve canal. The canals vls_3 and vls_4 join just at the postero-dorso-lateral corner of the orbit and the canals vls_5 and vls_6 unite into a rather long common trunk before opening into the canal *vcl*.

Remarks. — As appears from the description, given above, this form, although represented only by an imperfect cephalic shield, evidently belongs to the species *C. powriei* and most closely resembles its var. *asper;* it differs, however, from this variety in some respects (the broad cornua, the shape of the dorsal sensory field, and the ornamentation and the structure of the exoskeleton), and it seems most appropriate to regard it as a distinct variety, var. *polaris,* of *C. powriei.* If the var. *asper* is to be considered an independent species, as it was originally by Lankester (1870a, p. 50), the var. *polaris* must be placed as a variety of this species.

The Scottish species *C. powriei* is thus, by a new variety, represented also in the Old Red fauna of Spitsbergen, a remarkable fact, in so far as the known common Devonian forms of the faunal areas of Great Britain and of Spitsbergen are very few; the only other case is that of *C. cradleyensis* (cf. p. 580).

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Anglaspis horizon.

Locality. — Spitsbergen. E. side of Red Bay: W. of the Andrée Glacier, in the Anglaspis horizon.

The single specimen was collected by the ENS expedition in 1939.

21. *Cephalaspis eurynotus* n. sp.

(Fig. 44; pls. 18:2; 21:2.)

Diagnosis. — A *Cephalaspis* species of medium size with maximum breadth of cephalic shield about as great as length of shield in median line. Shield slightly narrowing anteriorly. Rostral margin broad, obtusely rounded. Cornua short and slender, projecting in posterior direction, reaching only slightly behind posterior end of interzonal part; their length constituting about one quarter of distance of their tips from rostral end of shield. Inner margins of cornua without denticles. Pectoral sinus deep and narrow. Inter-zonal part fairly short, rather high, broad; its breadth somewhat more than half of maximum breadth of shield. Dorsal sensory field elongate, rather narrow. Lateral sensory fields narrow, extending backwards only over proximal parts of cornua. Orbital openings rather small, situated somewhat in front of middle of length of shield in median line. Independent pineal plate present. Separate openings for nasal and for hypophyseal ducts. Superficial layer of exoskeleton continuous and smooth, without ornamentation. Middle layer with irregularly disposed radiating canals. Mucous canal system enclosed in exoskeleton, forming a very fine-meshed network.

Holotype. — Cephalic shield (ENS no. 531).

Material. — In the available material, this species is represented by two specimens (ENS no. 531, Pal. Mus. Oslo no. A30066).

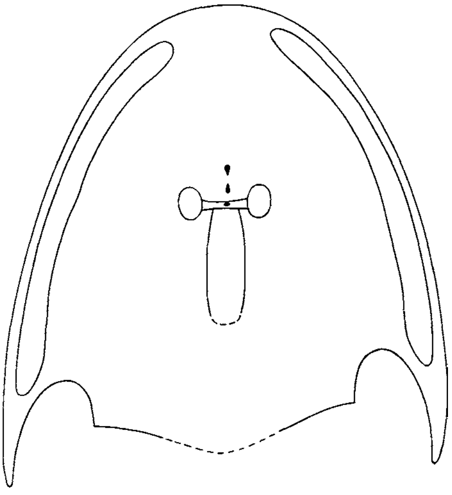


Fig. 44. — *Cephalaspis eurynotus* n. sp. Restoration of the cephalic shield, dorsal view. Mainly after the holotype (ENS no. 531). Nat. size.

The holotype (no. 531, pl. 18:2) consists of a fairly complete cephalic shield in counterpart, lacking the left cornu and a considerable portion of the inter-zonal part. The other specimen (no. A30066, pl. 21:2) consists of a cephalic shield, partly in counterpart, lacking the tip of the left cornu and rather much of the inter-zonal part; it is furthermore much distorted by pressure in the rock. In addition to these specimens, one specimen (ENS no. 532) is hesitatingly referred to this species; it consists of a very incomplete cephalic shield, lacking most of its central and posterior parts.

Description. — The holotype has the following dimensions. The length in the median line from the rostral end to the level of the posterior end of the preserved portion of the inter-zonal part is 57.5 mm, and the real length of the shield in the median line very probably was only slightly greater than this distance. The maximum breadth, which is situated between the posterior parts of the cornua, is estimated at 59 mm. The breadth of the inter-zonal part between the postero-lateral angles is 35 mm. The distance of the tip of the right cornu from the rostral end of the shield is 66.2 mm and the distance of the pineal fissure from the rostral end of the shield is 29 mm. The maximum height very probably lay as usual in the posterior portion of the inter-zonal part but as this part is incomplete it could not be measured; the height of the shield near the posterior end of the dorsal sensory field is 18.5 mm. The second shield and the shield hesitatingly placed here are of about the same size as the holotype shield. As seen from the measurements, the species attained only a medium size.

In its general shape the cephalic shield is narrow and rather high, its maximum breadth being about equal to its length in the median line. The shield narrows only slightly towards its anterior margin. The rostral margin is broad and broadly rounded, without any trace of a rostral angle and there are no angles at the transition of the rostral to the lateral margins. These latter are very slightly curved and continue backwards without any interruption into the margins of the cornua. The cornua project in a posterior direction and reach only for a short distance behind the posterior end of the inter-zonal part; they are very short in proportion to the size of the shield, and their length is contained about four times in the distance of their tips from the rostral end of the shield. The cornua are somewhat flattened dorso-ventrally in their proximal part but are almost cylindric distally; their inner borders are devoid of denticles. The pectoral sinus are deep and narrow and in the holotype provided with indistinct antero-median corners. The inter-zonal part is rather short and broad; its breadth between the postero-lateral angles constitutes about three-fifths of the maximum breadth. The postero-dorso-median portion of the inter-zonal part is missing in both specimens; to judge from the lines of fracture it does not seem improbable that the inter-zonal part was provided with a strongly developed dorsal spine, which, however, together with the adjacent parts of the shield had become detached before the fossilization. It is in any case evident that the inter-zonal part (the possible dorsal spine not included) was rather high and that its posterior end reached backwards only slightly behind the postero-lateral angles. The most posterior parts of the sensory field are not preserved, but with regard to the shape of the field it can be said that it is elongate and rather narrow, and was probably only slightly more than twice as long as broad, and that the distance of its posterior margin from the posterior end of the inter-zonal part was probably slightly greater than the length of the field. The lateral margins of the field are almost parallel and the anterior margin which lies immediately behind the pineal groove is rather broad and truncated. The lateral sensory fields are narrow and slightly increasing in breadth backwards, their posterior ends lie in the proximal third of the cornua. The distance between the antero-median ends of the two lateral fields is about twice as great as the inter-orbital breadth. The orbital openings, which are roundedly oval in shape and small in proportion to the size of the shield, are situated somewhat nearer to the rostral than to the posterior end of the shield, and at the same distance from the pectoral sinus as from the rostral end of the shield. The antorbital prominence is not very conspicuous. The pineal fissure is rather large and extends between the middle parts of the orbital openings. With regard to the circum-nasal fossa it is to be noticed that it lodges the separate openings for the nasal and for the hypophyseal ducts, and that it is narrow and rather deep, especially in its anterior parts.

The exoskeleton is rather imperfectly preserved. The superficial layer is continuous and apparently quite smooth without any ornamentation; the middle layer contains no quite regularly disposed radiating canals (pl. 21:2). The basal layer contains no ringsinus. The mucous canal system is enclosed in the exoskeleton and forms a very fine-meshed network without any differentiation into circum-areal and intra-areal canals.

The endoskeleton seems to be rather imperfectly developed, and of the internal structures only some of the superficial canals are indistinctly seen. It is, however, evident that the nerve canals to the lateral sensory fields behave as normally in the genus.

Remarks. — *C. eurynotus,* which is characterized by the narrowness of its shield, the broad and high inter-zonal part and the short cornua and the seperate openings for the nasal and hypophyseal ducts is suggestive of *C. lornensis* from the Lower Old Red Sandstone of Scotland (Traquair 1899a; Stensiö 1932, p. 118) and is probably rather closely related to this species. It differs from *C. lornensis* by a somewhat narrower shield, straighter lateral margins, broader rostral margin, longer and slenderer cornua and by the rather considerable height of the shield. It reminds furthermore remotely of *C. sollasi* (Stensiö 1932, p. 139) which is, however, larger than *C. eurynotus* and has a narrower rostral part of the shield and the cornua of different shape.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Anglaspis horizon.

Localities. — Spitsbergen. E. side of Red Bay: W. of the Andrée Glacier, in the Anglaspis horizon (no. 531), the shore profile, in talus (no. A30066). No. 532, hesitatingly placed here, is found on the Andrée Glacier, N. half, W. part, in the moraine.

No. A30066 was collected during Th. Vogt's expedition in 1928, the two other specimens (nos. 531—532) by the ENS expedition in 1939.

22. *Cephalaspis recticornis* n. sp.

(Fig. 45; pls. 20; 21:1, 3; 114:3.)

Diagnosis. — A *Cephalaspis* species of large size with maximum breadth of cephalic shield about one and a third times as great as length of shield in median line. Shield slightly narrowing anteriorly; rostral margin curved; antero-lateral margins strongly convex; lateral margins straight. Cornua very long and straight, projecting in posterior and slightly lateral direction, reaching far behind posterior end of inter-zonal part; length of cornua contained about twice in distance of their tips from rostral end of shield; median margins of cornua without denticles. Pectoral sinus deep. Inter-zonal part rather long; its breadth posteriorly constituting about two-fifths of maximum breadth of shield; dorsally with a low median ridge. Posterior end of inter-zonal part not or very slightly protracted behind postero-lateral angles. Dorsal sensory field about two and a half times as long as broad, slightly increasing in breadth towards posterior end, posterior margin of field truncated. Lateral sensory fields not reaching backwards over middle of length of cornua. Orbital openings small, situated in middle of length of shield in median line. No independent pineal plate present. Exoskeleton ornamented with tubercles of variable size and shape. Superficial layer continuous at least anteriorly on shield. Mucous canal system at least partly enclosed in exoskeleton, consisting of a fine-meshed network.

Holotype. — Cephalic shield (ENS no. 533).

Material. — In this species I place only three specimens (ENS nos. 533—535). The holotype (no. 533, pls. 20; 114:3) is a rather complete cephalic shield in counterpart, lacking parts of the antero-lateral margin and a dorso-posterior portion including the orbital openings; no. 534 (pl. 21:1) is an incomplete cephalic shield in counterpart, somewhat crushed and slightly distorted, wanting a great portion of its left half; no. 535 (pl. 21:3) is an incomplete cephalic shield in counterpart, lacking most of the left half, a postero-median portion, and the distal part of the right cornu.

Description. — The dimensions (in mm) of the shields are shown in the following table (figures in brackets are approximate):

Nos.	533	534	535
Length of shield in median line	(11)	13.3	—
Maximum breadth	(14.5)	(19)	—
Breadth of inter-zonal part, posteriorly	6.5	(7)	(6.5)
Distance of tip of cornu from rostral end of shield	17.3	(20.5)	—
Distance of pineal foramen from rostral end of shield	—	7.1	5.9
Distance of postero-lateral angle of inter-zonal part from rostral end of shield	11.1	12.9	11.6

The shields have thus belonged to a large-sized species.

The maximum breadth of the shield lies most posteriorly between the tips of the cornua and is about one and a third times as great as the length of the shield in median line. The shield narrows slightly in anterior direction and the rostral margin is rather strongly convex but there is no trace of a rostral angle. The antero-lateral margins, at the transition between the rostral and the lateral margins, are strongly curved, but the lateral margins are almost straight, and thus form a very acute angle with the longitudinal axis of the shield. The cornua, which are straight and very long, project in a posterior and slightly lateral direction, their outer margins forming straight continuations of the lateral margins of the main shield. The cornua are flattened dorsoventrally in their entire length. They reach very far behind the level

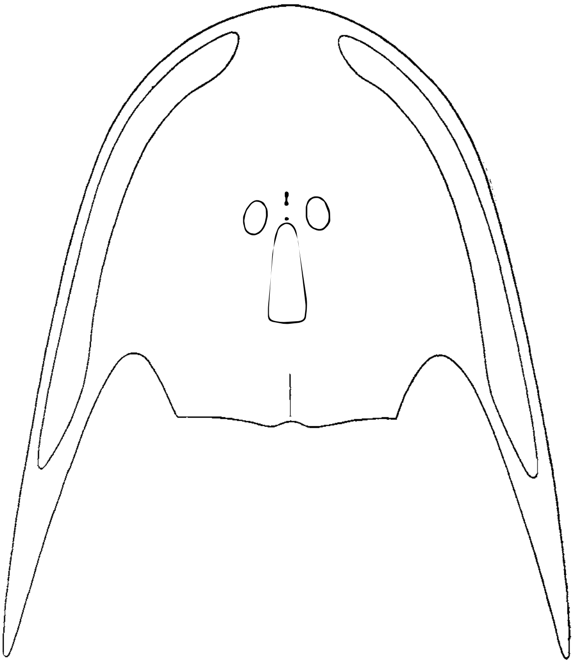


Fig. 45. — *Cephalaspis recticornis* n. sp. Restoration of the cephalic shield, dorsal view. After ENS nos. 533 and 534. ½.

of the posterior margin of the inter-zonal part; their length constitutes about half of the distance of their tips from the rostral end of the shield. There are no denticles along the inner margins of the cornua. The pectoral sinus are deep and fairly narrow. The inter-zonal part is rather long and high; its breadth decreases rapidly towards the postero-lateral angles, and is here contained about two and a half times in the maximum breadth of the shield and about twice in the median length of the shield. Dorsally the inter-zonal part is provided with a very low and inconspicuous median ridge. In no. 534 the dorso-median end of the inter-zonal part shows a distinct emargination. The posterior end lies at about the same level as or only very slightly behind the postero-lateral angles. The dorsal sensory field is about three times as long as broad with its greatest breadth at or near the posterior end; the anterior end of the field is rounded and the posterior margin truncated. The distance of the posterior margin of the field from the posterior end of the inter-zonal part is about equal to the length of field. The lateral sensory fields are fairly narrow but widen somewhat on the basal part of the cornua a short distance before their posterior end. They reach rather far backwards on the cornua and end just before the middle of the length of the cornua. The distance between the antero-median corners of the two fields is about three times as great as the inter-orbital breadth. The orbital openings are small in proportion to the size of the shield, are roundedly oval in shape and situated about midway between the rostral and the posterior ends of the main shield. The inter-orbital distance is about one and a half times as great as the transverse diameter of an orbital opening. The circum-orbital ridge seems to be rather narrow and inconspicuous; the antorbital prominence is comparatively small but well defined. No pineal plate is (or was) present. The naso-hypophyseal opening is normally developed and rather small; the fossa circum-nasalis is short and broad, rather shallow but fairly well defined.

In the holotype the exoskeleton is ornamented with tubercles, which on the anterior portion of the shield lie scattered and are rather wide, low, flattened, and not well defined; on the posterior portion of the shield they are more numerous, small, blunt and well defined. In no. 534 they are somewhat higher and some of them are pointed. In the holotype there is no apparent ornamentation on the ventral rim, the surface being only slightly rugose owing to the uneven rims around the openings of the mucous canals. In the holotype the superficial layer forms a continuous covering to the middle layer, in no. 534 the same conditions seem to prevail in the anterior parts of the shield while posteriorly the superficial layer in some places in the inter-tubercular spaces is entirely absent. The radiating canals in no. 534 are well developed and disposed in distinct bundles, six bundles originating from one batch of ascending canals, there are, in other words, six fascicles in each vascular area; the diameter of a vascular area is on the average 3 mm in the anterior part and 2.6 mm in the posterior part of the shield. In no. 535 (pl. 21:3) the vascular canals are more irregularly disposed, of varying calibres and often much branching, and thus somewhat reminding of those in *C. eurynotus.* There are no ringsinus in the basal layer, which is rather thin. At least in the holotype and probably anteriorly on the shield no. 534 the mucous canal system is enclosed in the exoskeleton; it is developed as a fine-meshed network of very fine-calibrated canals, and there is no distinction between circum-areal and intra-areal canals.

The endoskeleton is apparently very incompletely preserved, and besides many of the superficial canals only the orbital layer and traces of the linings of the postbranchial wall are observed in the holotype. The canals for the nerves of the lateral sensory fields are rather narrow and seem to be disposed as normally in the genus.

Remarks. — *C. recticornis* is very well characterized by the shape of its cephalic shield with the long straight cornua, and it cannot be confused with any of the other species of the genus. It seems not to be closely related to any of the known species of *Cephalaspis.* In the general shape of its shield, and disregarding the different shape of the cornua, *C. recticornis* is, however, somewhat reminiscent of *C. eurynotus.*

Geological horizon. Lower Eodevonian (Dittonian): Red Bay series, the Anglaspis horizon.

Localities. — Spitsbergen. W. side of Liefde Bay: Mt Pteraspis (nos. 533—534). E. side of Red Bay: Fraenkel Ridge, in the Anglaspis horizon (no. 535).

All the three specimens were collected during the ENS expedition in 1939.

23. *Cephalaspis platycephalus* n. sp.

(Fig. 46; pl. 22.)

1927. *Cephalaspis heintzii* in part, Stensiö, p. 270; pl. 35:1-2; (?) pl. 36:1.

Diagnosis. — A *Cephalaspis* species of medium size with maximum breadth of cephalic shield slightly less than twice as great as length of shield in median line. Shield strongly narrowing forwards. Rostral margin rounded, without rostral angle. Cornua rather slender and long, curved, projecting proximally in postero-lateral, distally in posterior direction; their length being contained somewhat more than twice in distance of their tips from rostral end of shield. Inner border of cornua without denticles. Pectoral sinus shallow and very wide. Inter-zonal part low, short and rather narrow, its breadth posteriorly about one-third of maximum breadth of shield; dorsally with very low median ridge. Postero-dorsal margin of inter-zonal part rounded, extending backwards somewhat behind postero-lateral angles. Dorsal sensory field comparatively small, about twice as long as broad. Lateral sensory fields reaching backwards over proximal parts of cornua. Orbital openings roundedly oval, situated in middle of length of shield in median line. No pineal plate. Exoskeleton with continuous superficial layer and probably without any tubercular ornamentations. Mucous canal system enclosed in exoskeleton and (probably) forming a fine-meshed plexus.

Holotype. — Cephalic shield (no. A30067) in the Palaeontological Museum, Oslo.

Material. — This species is represented by four specimens (Pal. Mus. Oslo nos. A30067—A30068 and ENS nos. 536—537). The holotype (no. A30067, pl. 22) and no. 536 consist of fairly complete cephalic shields in counterpart, nos. 537 and A30068 of fragmentary shields only. In addition to these specimens I place here with slight hesitation a specimen (ENS no. 538) consisting of an imperfectly preserved cephalic shield.

Description. — The shield has the following dimensions: The length from the rostral end to the posterior angle of the inter-zonal parts is 41 mm in the holotype and about 37 mm in no. 536, and estimated at about 40 mm in no. A30068. The maximum breadth, which in the holotype lies across the middle parts of the cornua, is here

72.5 mm and in no. 536, where it lies near to the tips of the cornua, 66 mm. The inter-zonal part is 25 mm broad in the holotype, 21 mm in no. 536 and about 26 mm in no. A30068. The maximum height is estimated at not more than 10 mm in the holotype. The specimen (no. 538) hesitatingly placed here is considerably smaller than the other specimens, the length of its shield is estimated at about 30 mm and the maximum breadth at about 53 mm. — The species was thus of moderate size.

The cephalic shield as a whole is very broad and flat and much narrowing forwards. The rostral margin of the shield is obtuse, fairly broad and convex without any trace of a rostral angle. The lateral margins are rather well curved. The cornua are long and rather slender, they are flattened dorso-ventrally and are curved in such a way that their basal parts project in a postero-lateral direction but their distal parts almost straightly backwards. The length of the cornua constitutes somewhat less than half of the distance of their tips from the rostral end of the shield. The inner margins of the cornua are devoid of denticles. The pectoral sinus are very broad and shallow; their antero-median corners are distinct although forming a very wide angle, any antero-lateral corners are on the other hand hardly discernable. The inter-zonal part is short and rather narrow, its breadth decreases rapidly backwards towards the postero-lateral angles and is here only about one-third of the maximum breadth of the shield. The postero-dorso-medial portion of the inter-zonal part is protracted backwards to some distance behind the level of the postero-lateral angles, and its posterior angle is rather sharply rounded. Dorsally, the inter-zonal part has a low median ridge, extending from a point somewhat behind the dorsal sensory field to the posterior end. The dorsal sensory field is rather small, elongated, and of about uniform breadth with very slightly convex lateral margins, and with rounded posterior margin; it is about half as broad as long. The distance of its posterior margin from the posterior end of the shield is about equal to the length of the field. The lateral sensory fields are rather broad; their lateral margins show a slight sinuosity in the posterior third of their length; the posterior termination of the fields on the cornua is not exposed in the fossils but the fields continue at least over the basal parts of the cornua. The orbital openings are roundedly oval and lie in the middle of the length of the shield in the median line. The circum-nasal fossa is very slightly pronounced. There was no independent pineal plate.

The exoskeleton of the shield is in a very poor state of preservation; it seems, however, probable that the superficial layer forms a continuous covering to the middle layer. Apparently the face of the exoskeleton in the holotype is smooth without any tubercular ornamentation, in nos. 236 and 537 some very small ill-defined tubercular

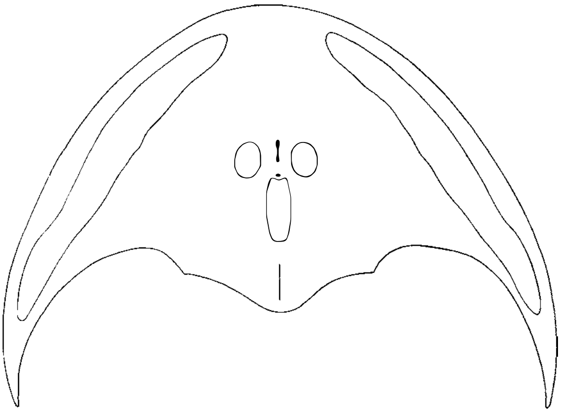


Fig. 46. — *Cephalaspis platycephalus* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (Pal. Mus. Oslo no. A30067). Nat. size.

elevations are observed on the lateral margins and on the cornua. Nothing of the mucous canals is directly seen, but they were probably enclosed in the exoskeleton and formed a fine-meshed network.

The endoskeleton is very imperfectly preserved in all the specimens; some of the superficial canals are seen in the holotype, and the nerve canals to the lateral sensory fields are disposed as normally in the genus.

Remarks. — *C. platycephalus* is most similar to *C. curta* (p. 382) from the Wood Bay series, and is possibly closely akin to this species; it differs in the large size of its cephalic shield, in the slenderer cornua, the narrower inter-zonal part, the smaller dorsal sensory field, etc. The species resembles furthermore to a certain degree *C. menoides* (p. 402) and *C. semicircularis* (p. 399) , but differs i. a. by the relatively greater length of its cephalic shield, which also is more narrowing anteriorly and has fairly slightly rounded lateral margins, and furthermore by the development of the lateral sensory fields. In the general shape of its shield, *C. platycephalus* is also somewhat reminiscent of *C. moy-thomasi* (p. 396). On the whole *C. platycephalus* reminds more of some of the species from the Wood Bay series than of any of the species from the Red Bay series.

The specimen (no. 538), hestitatingly placed in *C. platycephalus,* is badly preserved, but as far as can be seen agrees well with the other specimens of this species, except in its minor size.

C. platycephalus was originally included in *C. heintzi* by Stensiö (1927, p. 270) but it is now evident that it has nothing to do with this species. Of the original material of *C. heintzi,* no. 54 and very probably also no. 53 belong here.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the Ctenaspis and Benneviaspis horizons.

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, without indication of more exact locality (no. A30068, and no. 538, hesitatingly placed here), W. Plateau, in the Ctenaspis horizon (no. A30067); the Andrée Glacier, S. half, W. part, in the moraine (nos. 536—537).

The specimens nos. A30067—A30068 were collected by Th. Vogt's expedition in 1928, nos. 536—538 by the ENS expedition in 1939.

24. *Cephalaspis verruculosa* n. sp.

(Fig. 47; pls. 23:2; 24; 114:2.)

1927. *Cephalaspis spitsbergensis* in part, Stensiö, p. 276; fig. 71; pls. 35:3; 39; 40:2.

Diagnosis. — A *Cephalaspis* species of medium size with maximum breadth of cephalic shield slightly exceeding length of shield in median line. Shield narrowing anteriorly, rostral margin sharply rounded without any rostral angle. Lateral margins slightly curved. Cornua long and slender, projecting in posterior direction, reaching slightly behind posterior end of inter-zonal part (dorsal spine excluded), more or less slightly curved inwards; their length contained about two and two-thirds times in distance of their tips from rostral end of shield. Inner margins of cornua without denticles. Pectoral sinus moderately narrow and deep. Inter-zonal part broad, rather long and moderately high; its breadth contained about twice in maximum breadth of shield; dorsally with a rather high, acuminated, triangular median spine; posterior angle (at basis of dorsal spine) protracted backwards behind postero-lateral angles. Dorsal sensory field rather small, about twice as long as broad. Lateral sensory fields extending backwards to basal parts of cornua. Orbital openings situated in front of middle of length of shield in median line; circum-orbital rim well developed. Independent pineal plate present. Exoskeleton ornamented with numerous blunt tubercles of varying sizes. Superficial layer of exoskeleton only present in tops of tubercles. Mucous canal system not enclosed in exoskeleton.

Holotype. — Cephalic shield (no. A30069) in the Palaeontological Museum, Oslo.

Material. — The material referable to this species with a fair degree of certainty consists of six specimens (ENS nos. 539—540; Pal. Mus. Oslo nos. A30069—A30072). Five specimens (ENS nos. 541—542; Pal. Mus. Oslo nos. A30073—A30075) are placed here with a slight hesitation and three specimens (ENS nos. 543—544; Pal. Mus. Oslo no. A30076) are too fragmentary to allow of a definite specific determination and are thus only doubtfully assigned to this species. The preservation of the material is as follows. No. 539, rather complete shield in counterpart, lacking a small part of the left side with the cornu (pls. 24:2; 114:2). No. 540, rather complete shield in counterpart, without the left cornu (pl. 24:1). No. A30069 (the holotype) fairly complete shield wanting parts of the left side including the cornu (pl. 23:2). No. A30070, incomplete shield in counterpart, lacking a large portion of the median and the right parts. No. A30071, crushed and distorted shield in counterpart, lacking a portion of the left side. No. A30072, part of the left side of the shield in counterpart. Nos. 541—542, A30073—A30075, fragmentery shields. Nos. 543—544, A30076, shield fragments.

Description. — The dimensions (in mm) of some of the shields are given in the table below (figures in brackets are only approximate):

Nos.	539	540	A30069	A30070	A30071	A30072
Length in median line (from rostral end of shield to posterior end of inter-zonal part, at basis of dorsal spine)	51.5	57.6	57	—	53.5	—
Maximum breadth	(59)	(59)	(65)	—	(57)	—
Breadth of inter-zonal part between postero-lateral angles	(26)	28.4	(31.8)	—	—	—
Height of inter-zonal part (dorsal spine not included)	(18)	17	(20)	—	—	—
Distance of tip of cornu from rostral end of shield	67.8	67.5	67	62.7	—	60
Distance of pineal groove from rostral end of shield	23	24.3	22.3	—	—	(23)

The species was thus of medium size. The cephalic shield is rather slenderly built and its maximum breadth, which lies between the posterior halves of the cornua, is somewhat greater than the length of the shield in the median line. The shield decreases somewhat in breadth anteriorly and its rostral part is comparatively narrow. The rostral margin is sharply rounded but without any vestige of a rostral angle. The lateral margins are slightly curved and are inclined at a rather acute angle to the main axis of the shield. The cornua are long, slender and narrow, somewhat flattened at the bases but more or less circular in cross-section towards the apices. They project almost straightly backwards and generally reach slightly behind the level of the posterior angle of the shield; in no. 539 they extend somewhat farther backwards than in the holotype but in no. A30072 they are plainly shorter and stouter than in the other specimens. The cornua are generally only slightly curved but in nos. 539 and 540 they are bent distinctly inwards, in the former specimen, however, only near the apex. The length of the cornua constitutes about $^{3}/_{8}$ of the distance between their tips and the rostral end of the shield, in no. A30072 about one third of that distance. The median margins of the cornua are devoid of denticles (the tubercles present along the margins must not be confused with real denticles).

The pectoral sinus are comparatively narrow and deep; in no. 539 they are, however, distinctly shallower than in the others; they are on the whole broader and shallower in this species than in *C. sinuata.* The sinus are uniformly concave without any angles. The inter-zonal part is rather broad and long; its breadth between the postero-lateral angles is about half as great as the maximum breadth of the shield; it is moderately high and its height to the basis of the dorsal spine seems on the average to be about one-third of its breadth between the postero-lateral angles. The dorsal part is provided with a rather high median spine, which is shaped as an almost right-angled triangle with the acuminated apex slightly protracted backwards. The posterior angle of the inter-zonal part (at the basis of the dorsal spine) is very acute and protracted far behind the postero-lateral angles; the latter are obtuse when viewed from above. The dorsal sensory field is comparatively small, it is about twice as long as broad with the anterior and posterior margins truncated and the lateral margins slightly curved; the anterior margin lies immediately behind the pineal groove. The lateral sensory filds are rather narrow and continue backwards only over the basis of the cornua. The distance between the antero-median ends of the two fields is rather considerable in the holotype being about three times as great as the inter-orbital breadth but much less in nos. 539 and 540, being here only about twice as great as this distance. The orbital openings are rather small, oblong, and situated in front of the middle of the length of the shield in the median line; the distance of the pineal groove (which is situated between the middle parts of the orbital openings) from the posterior end of the shield is about one and a half times as great as its distance from the rostral end. The circum-orbital ridge is well developed as is also the antorbital prominence. The inter-orbital breadth is about one and a half times as great as the transverse diameter of an orbital opening. The pineal foramen was lodged in an (not preserved) independent pineal plate. The anterior portion of the naso-hypophyseal opening is situated at the bottom of a small but well defined circum-nasal fossa.

The exoskeleton is ornamented with numerous, rather blunt, verruca-like tubercles of varying sizes. Generally one large tubercle is situated dorsally to each group of ascending vascular canals and thus in the centre of a vascular or polygonal area but there are also tubercles of all sizes scattered between these central tubercles; the large central tubercle can occasionally be substituted by two or three small tubercles. The superficial layer is present only in the tubercles; in the inter-tubercular spaces only the lower part of the middle layer with the radiating vascular canals is found. The basal layer of the exoskeleton is well developed; no ringsinus have been observed. The vascular areas in the exoskeleton are rather varying in size and in the posterior parts of the

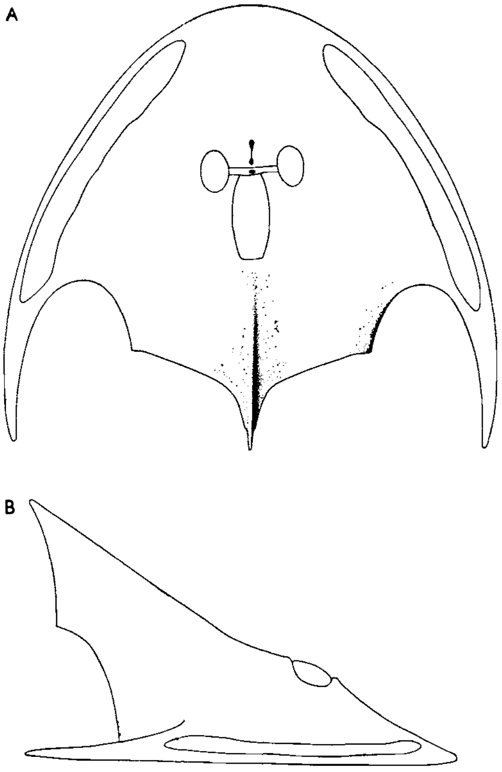


Fig. 47. — *Cephalaspis verruculosa* n. sp. Restoration of the cephalic shield, A, in dorsal, B, in lateral view. After the holotype (Pal. Mus. Oslo no. A30069). Nat. size.

shield seem to be about 1 mm in diameter (after measurements on the holotype and no. A30072). The mucous canal system was not enclosed in the exoskeleton and nothing can be said about its development.

The endoskeleton is on the whole poorly preserved; many of the superficial canal layers are, however, fairly well preserved. The canals for the nerves of the lateral sensory fields are disposed as normally in the genus, the first canal branches just antero-laterally to the orbit; the canals of the dorso-lateral superficial veins show some variation in their disposition; in no. 539, they are probably disposed as in no. 59 figured by Stensiö (1927, fig. 49; pl. 39), the canals vls_3 and vls_4 joining into a short common canal before opening into the canal *vcl* just at the postero-lateral corner of the orbit; the canal vls_6 receives a tributary from behind (vls_7) before joining the canal vls_5 and forming a common trunk, which opens into the canal *vcl* well behind the first common trunk. In the holotype the canals vls_5 and vls_6 join into a common trunk and this and the canals vls_4 and vls_7 converge towards a point just laterally to the canal *vcl* and it is possible that they all joined into a short common trunk which opened into this canal; the canal vls_3 opens directly into the dorso-lateral part of the orbit.

Remarks. — The species *C. verruculosa* is characterized by the general shape and proportions of its shield, by the slender cornua, the shape of the inter-zonal part with its dorsal spine, and by the ornamentation of the exoskeleton. It is somewhat suggestive of *C. sinuata* a species of about the same size, which, however, differs by its broader shield, shorter and stouter cornua, very narrow pectoral sinus and a differently shaped inter-zonal part. From *C. spitsbergensis* (Stensiö 1927, p. 276) and *C. tenuicornis* (p. 338), which it resembles in the general shape of the shield, it is distinguished first of all by its much smaller size; the shield of *C. spitsbergensis,* which is rather imperfectly known, is broader and has much longer and slenderer cornua than in *C. verruculosa; C. tenuicornis* differs by the broader and shallover pectoral sinus and the narrower inter-zonal part, the lateral sensory fields are, in addition, more strongly developed than in *C. verruculosa.* This species shows some remote likeness to *C. gracilis* (Stensiö 1927, p. 279), but in this species the cornua are much longer and straighter and provided with denticles on their inner margins. According to our present knowledge the species mentioned above seem to be the closest relatives to *C. verruculosa* among the *Cephalaspis* species known.

In *C. verruculosa* I place the specimen no. 59 in the Palaeontological Museum, Oslo; it was provisionally referred to *C. spitsbergensis* by Stensiö (1927, p. 276).

Geological horizons. — Lower Eodevonian: Red Bay series, the Primaeva horizon, (?) the Anglaspis horizon.

Localities. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Primaeva horizon (nos. 539—540, 543—544, A30069—A30076); W. of the Andrée Glacier, in the Anglaspis horizon (no. 542); the Andrée Glacier, N. half, W. part, in the moraine (no. 541; *obs.* the two last-mentioned specimens are placed with some doubt in this species).

The specimens nos. A30069—A30076 were collected by Th. Vogt's expedition in 1928; the others by the ENS Spitsbergen expedition in 1939.

25. *Cephalaspis sinuata* n. sp.

(Fig. 48; pls. 23:1; 25:2-3.)

Diagnosis. — A *Cephalaspis* species of medium size with maximum breadth of cephalic shield somewhat greater than length of shield in median line; shield rather broad anteriorly; rostral margin obtusely rounded. Cornua rather long and stout, projecting in posterior direction, reaching behind level of posterior end of inter-zonal part; their length contained about three times in distance of their tips from rostral end of shield; inner margin of cornua without denticles. Pectoral sinus deep and very narrow. Inter-zonal part very broad; its breadth constituting about two-thirds of maximum breadth of shield; rather high with a median, rather low, backwardly inclined, acuminated dorsal

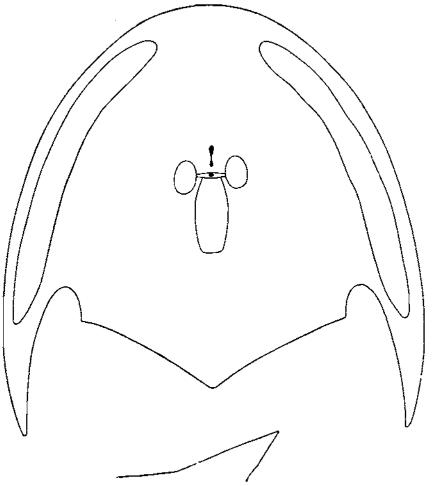


Fig. 48. — *Cephalaspis sinuata* n. sp. Restoration of the cephalic shield, dorsal view; *below:* dorsal spine in profile. After ENS nos. 545—546 and Pal. Mus. Oslo no. A30077. Nat. size.

spine; posterior angle protracted backwards well behind postero-lateral angles. Dorsal sensory field small, about twice as long as broad; posterior margin truncated. Lateral sensory fields extending backwards to basal parts of cornua. Orbital openings situated in front of middle of length of shield in median line. Independent pineal plate present. Exoskeleton smooth, without ornamentation (or in places with small blunt tubercles). Superficial layer apparently continuous. Mucous canal system forming a fine-meshed network, wholly (or partly) enclosed in exoskeleton.

Holotype. — Cephalic shield (ENS no. 546).

Material. — To this species I refer seven specimens (ENS nos. 545—548, Pal. Mus. Oslo nos. A30077—A30079). They all consist of imperfectly preserved cephalic shields; the holotype (no. 546; pl. 25:2-3) is rather complete, lacking an antero-lateral portion of the shield, no. 548 also is fairly complete, nos. 545 (pl. 23:1), A30077—A30078 are devoid of most of the right half of the shield, no. 547 lacks a major part of the left side and is furthermore somewhat affected by pressure of the rock; no. A30079 is more fragmentary still. With some hesitation I place here three fragmentary specimens (ENS no. 549; Pal. Mus. Oslo nos. A30080—A30081). Two specimens (ENS no. 550; Pal. Mus. Oslo no. A30082) are represented by fragments which do not permit a definite specific identification and are placed here with much doubt.

Description. — The specimens are not particularly well preserved and only a few direct measurements can be taken. The length of the cephalic shield (from the rostral end to the tip of the dorsal spine) in the holotype is estimated at about 50 mm; its maximum breadth which lies across the basal parts of the cornua, is 55 mm; the breadth of the inter-zonal part between its postero-lateral angles is 34.5 mm, its height to the basis of the dorsal spine is roughly estimated at 11 mm. The distance of the pineal groove from the tip of the dorsal spine is 30 mm.

In no. 545 the maximum breadth of the shield is estimated at about 57 mm, the breadth of the inter-zonal part at about 38 mm, and the distance of the pineal groove from the tip of the dorsal spine is 31 mm. The other specimens seem to be of about the same size but are too imperfectly preserved as to allow of exact measurements or any positive estimations to be taken. No. 548, which is rather well preserved, is of somewhat larger size, as is seen from the following measurements: length of shield in median line about 61 mm, maximum breadth 69 mm, breadth of inter-zonal part 32 mm, distance of tip of cornu from rostral end of shield 79 mm, distance of pineal groove from rostral end of shield 29 mm, and from posterior end of shield (dorsal spine not included) about 31 mm. — The species was thus of a medium size.

The maximum breadth of the shield lies between the basal parts of the cornua and is somewhat greater than the median length of the shield. The rostral margin is obtusely rounded without any rostral angle, and passes without interruption into the lateral margins, which are also curved. The cornua are fairly long and stout, they are flattened dorso-ventrally in their entire length and not, as in *C. verruculosa,* rounded in cross-section towards their tips. In the holotype and in no. 545 the outer margins of the cornua are somewhat curved while the inner margins are rather straight. The cornua project in a posterior direction and reach quite a distance behind the posterior end of the inter-zonal part. The length of the cornua constitutes about one-third of the distance of their tips from the rostral end of the shield. The inner margins of the cornua are devoid of denticles. The pectoral sinus are very characteristically shaped; they are deep and comparatively very narrow; the bottom of the sinus is often slightly asymmetrical with the greatest depth near the median side. The inter-zonal part is moderately long, rather high, and very broad; its breadth between the postero-lateral angles is contained almost one and a half times in the maximum breadth of the shield. The dorso-median portion is provided with a rather low, somewhat backwardly protracted, triangularly acuminated, dorsal spine. The posterior angle of the inter-zonal part (at the basis of the dorsal spine) is obtuse and protracted backwards well behind the postero-lateral angles; in no. 548, however, the posterior angle lies only slightly posteriorly to the postero-lateral angles; this condition is possibly explained by the fact that the posterior parts of this shield are somewhat compressed and distorted. The dorsal sensory field is rather small and about twice as long as broad; the anterior and posterior margins are truncated, the posterior one is somewhat rounded; the lateral margins are slightly convex; the anterior margin lies immediately behind the pineal groove. The lateral sensory fields are of normal breadth and reach backwards on to the proximal part of the cornua; the distance between their antero-median corners is somewhat variable, in the holotype about twice as great as the inter-orbital breadth, in no. 545 about three times as great as this distance. The orbital openings are rather small, rounded or roundedly oval in shape, and situated slightly (nos. 547—548) or definitely (nos. 545—546) in front of the middle of the length of the shield. A narrow but distinct circum-orbital ridge is present (well displayed in nos. 545, A30081); the antorbital prominences are rather inconspicuous. The inter-orbital space is about one and a half times as broad as the transverse diameter of an orbital opening. The pineal foramen was in the living animal situated in an independent pineal plate. The naso-hypophyseal opening is rather oblong, the circumnasal fossa is long and shallow, even in its anterior division.

The exoskeleton is very difficult to examine, at least with regard to its outer parts. There seems to be no ornamentation or a very feeble one on its outer face; in the holotype a few very small tubercles are observed near the orbital openings, in no. 545, however, as far as observed, the surface of the exoskeleton is smooth. The superficial layer of the exoskeleton is apparently very delicate and thin; in no. 545, at least, it forms a continuous covering to the middle layer, and this is probably the case also in the holotype. The middle and the basal layers are well developed. The radiating canals are well displayed in the holotype and in no. 545, where they are forming rather incompletely separated vascular areas, one or two of the canals in a vascular area being of a much coarser calibre than the others. The diameter of a vascular area in the holotype is in general 1.4 mm. The mucous canal system is enclosed in the exoskeleton, at least in no. 545; it forms a fine-meshed network without any differentiation between circum-areal and intra-areal canals.

Of the endoskeleton only the canals of superficial vessels and nerves have been observed; in no. 545 also a dorsal part of the orbital layer is seen; as to the rest the endoskeleton seems to be very slightly or not at all preserved. The canals vls_4 and vls_5 join into a rather long common trunk which opens into the canal *vcl*, as observed in no. 546; the canal vls_3 and the canals for the nerves of the lateral sensory fields are normally developed.

Remarks. — *C. sinuata* is characterized particularly by the peculiarly shaped pectoral sinus, to a lesser degree by the general shape of the shield, the broad inter-zonal part, and the low dorsal spine. It is fairly well separated from all other known *Cephalaspis* species but seems to be more closely related to *C. verruculosa* (p. 330), *C. tenuicornis,* and perhaps *C. spitsbergensis* (Stensiö 1927, p. 276). In the general shape of its shield it somewhat resembles *C. verruculosa* but this species has an anteriorly narrower shield, slenderer cornua, broader pectoral sinus, narrower inter-zonal part, etc. *C. tenuicornis* is a much larger species than *C. sinuata* and has a more triangular shield with much narrower rostral part, and the cornua and the pectoral sinus are differently shaped, etc.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the Primaeva and Anglaspis horizons.

Localities. — Spitsbergen. W. side of Liefde Bay: Mt Pteraspis (nos. 546—547). E. side of Red Bay: Fraenkel Ridge, in the Primaeva horizon (nos. 545, 549—550, A30077—A30082); W. of the Andrée Glacier, in the Anglaspis horizon (no. 548).

The specimens nos. A30077—A30082 were collected by Th. Vogt's expedition in 1928, the others by the ENS expedition in 1939.

26. *Cephalaspis tenuicornis* n. sp.

(Fig. 49; pl. 26:1.)

Diagnosis. — A large *Cephalaspis* species with maximum breadth of cephalic shield about one and a third times as great as length of shield in median line. Rostral part of shield narrow; rostral margin sharply rounded without rostral angle. Cornua long and very slender, distally almost cylindrical, projecting in posterior direction, reaching behind posterior end of inter-zonal part, curved slightly inwards. Length of cornua contained almost three times in distance of their tips from rostral end of shield. Inner margins of cornua without denticles. Pectoral sinus broad and rather deep. Inter-zonal part moderately long and broad; its breadth constituting about two-fifths of maximum breadth of shield. Dorsal sensory field about twice as long as broad, posterior margin truncated. Lateral sensory fields extending on to proximal part of cornua, anteriorly narrow behind a widened foremost part, rather broad in posterior half. Orbital openings small, situated distinctly in front of middle of length of shield in median line. Anterior division of circum-areal fossa very deep. No independent pineal plate. Ornamentation of exoskeleton consisting of numerous rather small tubercles. Mucous canal system situated superficially to exoskeleton in circumtubercular grooves. Polygonal areas very small in proportion to size of shield.

Holotype. — Cephalic shield (ENS no. 552).

Material. — This species is represented with certainty by four specimens (ENS nos. 551—552 and Pal. Mus. Oslo nos. A21500, A30083). The holotype (no. 552, pl. 26:1) consists of a rather complete cephalic shield, partly in counterpart, lacking a considerable portion of its postero-median parts; nos. 551, A30083 also consist of imperfect shields, lacking most of the inter-zonal parts; no. A21500 consists of a shield, lacking its left and its anterior parts. In addition to these specimens I place here with some hesitation two specimens (ENS nos.

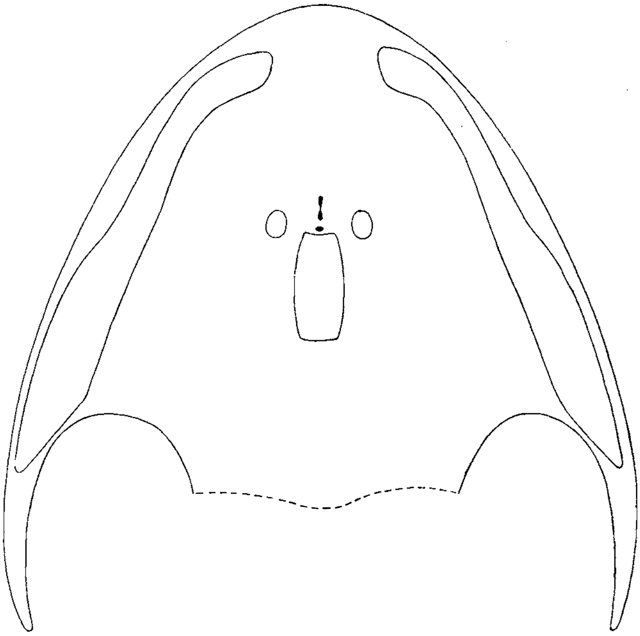


Fig. 49. — *Cephalaspis tenuicornis* n. sp. Restoration of the cephalic shield; dorsal view. After the holotype (ENS no. 552). ½.

553—554); the first (no. 553) consists only of a single cornu with adjacent parts, the second (no. 554) of a part of the left side of a cephalic shield.

Description. — The dimensions of the holotype shield are as follows. The real length could not be measured as the postero-dorso-median portion of the inter-zonal part is missing; the length from the rostral end to the level of the postero-lateral angles of the inter-zonal part (in the median line) is, however, 12.9 cm, and it seems probable that this distance corresponds approximately to the original length of the shield in the median line. The maximum breadth which lies between the middle parts of the cornua amounts to 17 cm. The height of the shield, measured at the posterior part of the dorsal sensory field, is about 5.3 cm, but the maximum height was with certainty slightly greater and lay farther backwards. The breadth of the inter-zonal part between the postero-lateral angles is about 7.1 cm. The distance of the rostral end of the shield from the tip of the left cornu measures 18.5 cm, and from the pineal foramen 6.7 cm. No exact measurements can be taken on the other shields; they seem, however, to be of almost the same size as the holotype; in no. A21500 the height of the inter-zonal part at its posterior end is about 4.3 cm.

In general shape the cephalic shield is moderately broad; its maximum breadth is somewhat greater than the length of the shield in the median line, or about one and a third times exceeding that length. The shield is rather rapidly decreasing in breadth anteriorly, its rostral parts being thus comparatively narrow; the rostral margin is convex and uniformly curved without any rostral angle. The lateral margins of the main shield are slightly convex and there are no angles at their transition into the rostral margin nor are there any concavities (or very slight ones) or angles at the bases of the cornua but the margins pass without interruption into those of the cornua. In no. A30083 the lateral margins of the main shield are almost straight in their middle parts. The cornua, which are long and very slender, project in a posterior direction and reach probably rather far behind the posterior end of the inter-zonal part; their length constitutes somewhat more than one-third of the distance of their tips from the rostral end of the shield, and probably about half the length of the shield in the median line. The cornua are somewhat flattened dorso-ventrally in their proximal parts but almost cylindrical in their distal halves. Their posterior parts are slightly curved in median direction. The inner margins of the cornua are not provided with any denticles. The pectoral sinus are rather broad and deep, and are almost uniformly concave. The inter-zonal part is moderately long and broad, and somewhat decreasing in breadth backwards; its breadth between the postero-lateral angles is somewhat less than half the maximum breadth of the shield. The height of the inter-zonal part seems to be rather considerable. The configuration of the dorsal portion of the inter-zonal part and the shape of its posterior margin are unknown in most of the specimens, including the holotype. In no. A21500, however, the inter-zonal part is fairly complete, its posterior end seems to lie at about the same transverse level as the postero-lateral angles, and it is provided with a probably rather low and indistinctly marked dorsal median ridge. The dorsal sensory field is about one and a half times as long as broad, with the lateral margins slightly bent; the transverse, truncated or slightly concave anterior margin lies closely behind the pineal foramen; the posterior margin is truncated. The distance of the posterior margin of the field from the posterior end of the shield could not be measured but it is evidently considerably greater than the length of the field. The lateral sensory fields are narrow in their anterior halves; most anteriorly they are, however, somewhat widened at the branching point of the first nerve canal for these fields. At the middle of their length the fields increase rather suddenly in breadth as a result of their lateral margins approaching the margins of the shield; their maximum breadth lies just anteriorly to the pectoral sinus and here the median margins of the fields sometimes form a very obtuse and indistinct postero-median angle pointing towards the shoulder-girdle. The fields reach backwards only over the basal parts of the cornua. The distance of the antero-median ends of the two fields is about equal to the distance between the centres of the two orbital openings. The orbital openings, which are remarkably small in proportion to the size of the shield, are almost circular or roundedly oval in shape and situated before the middle of the length of the shield in the median line; the distance of an orbital opening from the rostral end of the shield is about equal to its distance from the pectoral sinus of its side. The orbital openings are surrounded by very strongly developed and thick circum-orbital ridges; the antorbital prominences are rather well defined. The pineal foramen is situated between the middle parts of the orbital openings; it was not lodged in a pineal plate. The posterior division of the naso-hypophyseal opening is placed on a narrow, rather prominent elevation; the anterior division, on the contrary, in the very deep anterior part of the circum-nasal fossa.

The exoskeleton is ornamented with numerous rather small, flattened tubercles. The superficial and the outer division of the middle layer are discontinuous and present in the tubercles only. The lower division of the middle layer has well developed radiating canals of fine calibres, disposed in rather regular, small, vascular areas; each group of ascending canals is situated beneath a tubercle, which thus indicates the centre of a vascular area. The basal layer is comparatively thin and its lower face is provided with rather wide grooves forming polygonal figures and evidently corresponding to the ringsinus in other species. The mucous canal system was not enclosed in the exoskeleton but lay outside of it and very probably in the inter-tubercular grooves; nothing more can, however, be said of its development. The polygonal areas formed by the inter-tubercular grooves and the ringsinus-like grooves and which correspond to the vascular areas are very small in proportion to the size of the shield, their average size being 1.9 mm in diameter.

The endoskeleton seems to be very imperfectly developed in the holotype and no. 551, in which only traces of the perichondrial bone-layers lining the canals in the lateral sensory fields are seen. In no. A30083 the endoskeleton is rather well ossified and parts of the internal and orbital layers as well as parts of the external layer lining the oralobranchial chamber and the posterior face of the pectoral area are observed. The bone-layers of the superficial canals are, however, imperfectly preserved and nothing can be said with any certainty of the proximal courses of the canals for the dorso-lateral superficial veins; the canals for the nerves to the lateral sensory fields are disposed as normally in the genus.

Remarks. — *C. tenuicornis* is characterized by the size and proportions of its shield and the long and slender, slightly curved cornua in conjunction with the very small polygonal areas in the exoskeleton. Shields displaying these features are fairly easily distinguished from their congeners. The species seems to be most closely related to *C. verru-*

culosa (p. 330), *C. sinuata* (p. 334), *and* possibly to *C. spitsbergensis* (Stensiö 1927, p. 276) and *C. crofti* (p. 344). It is much greater than these species, and differs furthermore from *C. verruculosa* and *C. sinuata* by the configuration of the inter-zonal part, the shape of the sensory fields, the very small orbital openings, the absence of a pineal plate, etc., and from *C. crofti* by the narrower anterior part of the shield, the lateral margins of the shield not being concave at the basis of the cornua, and by the shallower pectoral sinus. The shape of the cornua is somewhat similar in *C. tenuicornis* and in *Tegaspis kolleri* (p. 438) and shield fragments with cornua of the two species may be mixed up, but in the latter species the cornua are broader than in the former and the lateral sensory fields do not enter the cornua; the polygonal areas are furthermore much larger in *T. kolleri* than in *C. tenuicornis.*

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the upper parts (the Ben Nevis division).

Localities. — Spitsbergen. E. side of Red Bay: the Andrée Glacier, in the moraine (no. A21500); the Andrée Glacier, S. half, W. part, in the moraine (nos. 551—552); Mt Ben Nevis, the Second Glacier, in the moraine ("the Cephalaspis moraine"; no. A30083). The specimens, somewhat doubtfully referred to this species were found — no. 553 on Mt Ben Nevis, no. 554 on the Andrée Glacier, S. half, W. part, in the moraine.

The specimens nos. A21500 and A30083 were collected during Th. Vogt's expedition in 1928, nos 551—554 during the ENS expedition in 1939.

27. *Cephalaspis arcticus* Stensiö.

(Pl. 25:1.)

1927. *Cephalaspis arcticus,* Stensiö, p. 280; fig. 74; pl. 38:1 (not pls. 24:2; 28; 37:4; 40:5).

Diagnosis. — A *Cephalaspis* species of medium size, with maximum breadth of cephalic shield (probably) about one and a half times as great as length of shield in median line. Shield rather strongly narrowing anteriorly. Rostral margin narrow, convex, without rostral angle. Cornua long and slender, curved, projecting, the basal parts in postero-lateral, the distal parts in posterior direction. Length of cornua (probably) contained slightly more than twice in distance of their tips from rostral end of shield. Inter-zonal part broad; its breadth about one-half as great as maximum breadth of shield. Dorsal sensory field small, about one and a half times as long as broad, with greatest breadth in anterior half of its length. Lateral sensory field ending posteriorly on basal half of cornu. No pineal plate. Exoskeleton ornamented with small rather high, blunt or pointed tubercles.

Holotype. — Cephalic shield (no. 66) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 280).

Material. — In this species I place one specimen (ENS no. 555); it consists of an imperfectly preserved cephalic shield, the median parts of which are much worn and abraded; the distal parts of the cornua are lacking.

Remarks. — As far as the state of preservation of the present specimen allows a comparison it agrees with the holotype in the size and proportions of the shield, and in the development of the ornamentation of the exoskeleton, and I thus place it with a fair degree of certainty in the species *C. arcticus.*

The length in the median line of the shield from the rostral end to the level of the preserved postero-lateral portion of the inter-zonal part is 40 mm; the maximum breadth of the shield is estimated at 60 mm; the shield is thus slightly smaller than the holotype. Since the new specimen is very imperfectly preserved it contributes but little to the knowledge of the species. Thus it is seen that the rostral margin is rather sharply rounded and without any rostral angle, the rostral margin being somewhat more protracted anteriorly and more rounded than in the restoration given by Stensiö (1927, fig. 74). On the rostral and lateral margins of the shield the exoskeleton is ornamented with numerous small but comparatively high tubercles, some of them being rather bluntly rounded. while others are more pointed; the "small straight denticles" observed in the holotype on the median and lateral margins of the cornua (Stensiö 1927, p. 281) are of the same kind as the tubercles on the rostral and lateral margins of the shield, and form a continuation of this tuberculation backwards on to the cornua. The inner margins of the cornua are thus devoid of real denticles. The minute structure of the exoskeleton is rather obscure but it seems likely that the superficial layer is discontinuous and only present in the tubercles. Nothing has been observed of the mucous canal system, and it seems probable that it was situated entirely outside the exoskeleton.

In the general outlines of its shield *C. arcticus* is somewhat suggestive of *C. watsoni* (Stensiö 1932, p. 136), *C. crofti* (p. 344), *C. heintzi* (p. 281) and *C. verruculosa* (p. 330); the differences between *C. arcticus* and *C. watsoni* are pointed out by Stensiö (1932, p. 138); from *C. crofti* the present species differs by the narrower rostral margin, by the lateral margins not being concave at the bases of the cornua, the broader cornua, and by the smaller size of the shield; from *C. heintzi* it differs i. a. by the greater size, the smaller orbital openings, and the slenderer cornua, devoid of denticles. From *C. verruculosa* it differs by the shorter and broader shield, the shape of the cornua and the dorsal sensory field and by the ornamentation of the exoskeleton.

The two specimens (nos. 67, 69), hesitatingly placed in this species by Stensiö (1927, p. 280), do not belong here; no. 67 is a *Cephalaspis,* no. 69 a *Benneviaspis,* both indeterminable as to species.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Polaris horizon.

Locality. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Polaris horizon. (The holotype was found on the Fraenkel Ridge, in a horizon 250 m above sea-level, see Stensiö 1927, p. 282; this horizon corresponds to the Polaris horizon, cf. Kiær & Heintz 1935, p. 13.)

The single specimen was collected by the ENS expedition in 1939.

28. *Cephalaspis crofti* n. sp.

(Fig. 50; pl. 26:2.)

Diagnosis. — A *Cephalaspis* species of fairly large size with maximum breadth of cephalic shield about one and a half times as great as length of shield in median line. Lateral margins of shield slightly concave at bases of cornua. Rostral margin broad, obtusely rounded without rostral angle. Cornua long and slender, projecting in proximal parts in postero-lateral, in distal parts in posterior direction, rather strongly curved; length of cornua contained slightly more than twice in distance of their tips from rostral end of shield. Pectoral sinus well defined, rather broad and deep. Inter-zonal part rather long and high, moderately broad; its breadth constituting about two-fifths of maximum breadth of shield. Exoskeleton ornamented with comparatively small tubercles along rostral and lateral margins and on ventral side of shield.

Holotype. — Cephalic shield (no. A30084) in the Palaeontological Museum, Oslo.

Material. — The material, which can be referred with certainty to this species consists of the holotype (Pal. Mus. Oslo no. A30084) only. In addition to this specimen, I place here with some hesitation another specimen (ENS no. 556). The holotype (pl. 26:2) consists of a fairly complete cephalic shield (lacking a considerable portion of the middle and posterior parts of the shield) but is much weathered and abraded; no. 556 is a very imperfectly preserved but otherwise rather complete shield, which only lacks the cornua.

Description. — The holotype has the following dimensions: The length of the cephalic shield in the median line could not be directly measured as the dorso-median portion of the inter-zonal part is missing, but it can be estimated at about 85 mm. The maximum breadth of the shield, which lies between the middle parts of the cornua, is 126 mm, and the breadth of the inter-zonal part between the postero-lateral angles amounts to 49 mm. The distance of the pineal foramen from the rostral

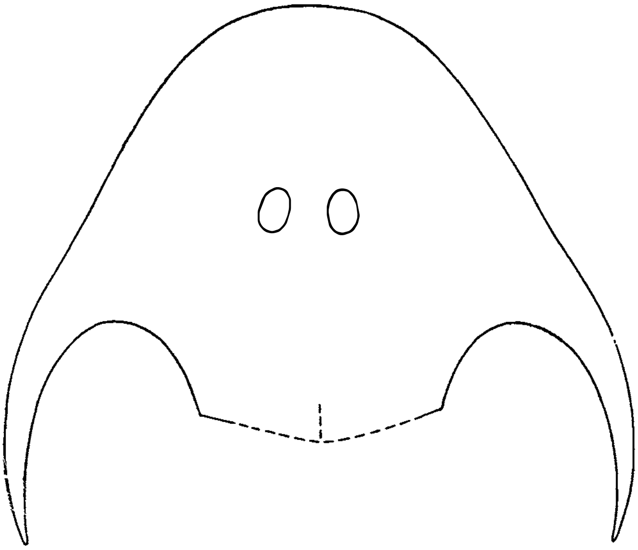


Fig. 50. — *Cephalaspis crofti* n. sp. Partial restoration of the cephalic shield, dorsal view (the sensory fields, the naso-hypophyseal and the pineal openings omitted). After the holotype (Pal. Mus. Oslo no. A30084). ⅔.

end of the shield is estimated at 43 mm. The height of the shield at a point somewhat posterior to the orbits is 26 mm. In no. 556 the length of the shield in the median line is 77 mm, and the breadth of the inter-zonal part 41 mm; the distance of the pineal foramen from the rostral end of the shield is estimated at 43 mm. The maximum height at the posterior end of the inter-zonal part is about 25 mm. This shield is thus somewhat smaller than that of the holotype.

The following description refers to the holotype only. On the whole, the cephalic shield is rather broad with the maximum breadth about one and a half times as great as the length of the shield in the median line. The breadth decreases rather rapidly anteriorly. The rostral margin is, however, broad, being about as broad as the inter-zonal part, and is in addition rather obtusely rounded without any trace of a rostral angle. The lateral margins of the main shield are almost straight but somewhat concave before the bases of the cornua. The cornua are rather strongly curved, their basal parts project from the main shield in a postero-lateral direction, their distal parts are directed more straightly posteriorly and their tips are slightly curved medially. The cornua are long and slender and reach far behind the inter-zonal part; their length is slightly less than half of the distance of their tips from the rostral end of the shield. As they are much abraded it is impossible to say whether their inner margins were provided with denticles or not. The pectoral sinus are rather broad and deep, they are uniformly concave without any corners. The inter-zonal part is comparatively long and high, its breadth is but moderate and contained about two and a half times in the maximum breadth of the shield. As the dorso-median portion is lacking in the holotype it cannot be stated whether there was a dorsal median spine or not. Nothing is preserved of the sensory fields; the dorsal field, however, seems to have been rather narrow. The orbital openings, which are oblong in shape, are situated somewhat nearer to the rostral than to the posterior end of the shield, and the distance of the openings from the pectoral sinus is about the same as that from the rostral end.

The exoskeleton is very imperfectly preserved and it is impossible to say whether the superficial layer is continuous or not; the ornamentation along the rostral and lateral margins and on the ventral side of the shield consists of small, blunt or somewhat pointed tubercles. In the middle layer there are normally developed radiating canals. The development of the mucous canal system is unknown.

The endoskeleton was rather slightly ossified. Traces of the canals of the first and second nerves for the lateral sensory fields are observed on the left half of the shield; they behave as normally in *Cephalaspis*. The anterior and the right parts of the shield are much abraded and several of the internal structures in the visceral endoskeleton are thus exposed.

The specimen (no. 556), doubtfully referred to this species has a shield of about the same general shape as the holotype, but as the cornua are not preserved, their shape could not be ascertained. It can be observed that the orbital openings lie rather far backwards, in fact slightly nearer to the posterior than to the rostral end of the shield. In this specimen the shape of the inter-zonal part of the shield is displayed: the posterior angle reaches backwards only for some distance behind the postero-lateral angles; dorsally the inter-zonal part is provided with a very short and indistinct median ridge just before the posterior end. The dorsal sensory field is about twice as long as broad but its exact shape cannot be determined. The ornamentation of the exoskeleton (as far as observed) consists of tubercles of varying size and shape, some broad and flattened. The outer parts of the exoskeleton are subdivided into small polygonal areas with an average diameter of 1.9 mm.

Remarks. — This species is rather similar to *C. arcticus* (p. 342 and Stensiö 1927, p. 280) and *C. tenuicornis* (p. 338), differing from the former by the large size of its shield, the more markedly curved cornua, the broad pectoral sinus and the broad rostral margin, from the latter species by the smaller size of the shield, the broad rostral margin, and the slightly concave lateral margin.

The specimen, doubtfully referred to *C. crofti*, although very imperfectly preserved, is placed here because it exhibits certain similarities with that species in the shape of the shield. It differs, however, by the size of its shield and by some other details from the holotype. It is therefore possible that in the future with an increasing knowledge of this and related species, the specimen will prove to represent a different species.

The species *C. crofti* is named in honour of Mr. W. Croft, London, palaeo-botanist, who was a member of the ENS expedition to Spitsbergen in 1939.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the upper parts (the Ben Nevis division).

Localities. — Spitsbergen. E.side of Red Bay: Mt Ben Nevis, in talus (no. 556); in the debris at the Cliff ("below the S. plateau"; no. A30084).

No. A30084 (the holotype) was collected by Th. Vogt's expedition in 1928, no. 556 by the ENS expedition in 1939.

29. *Cephalaspis signata* n. sp.

(Fig. 51; pls. 27:2; 28:1; 29—31; 32:1-3; 33:3; 35:3; 114:1.)

? 1927. *Cephalaspis spitsbergensis,* Stensiö 1927, p. 276; pl. 33:1.

Diagnosis. — A *Cephalaspis* species of rather large size, with maximum breadth of cephalic shield about one and a third times as great as length of shield in median line. Shield moderately narrowing forwards, rostral part rather broad; rostral margin obtusely curved without rostral angle. Lateral margins almost straight. Cornua very long and slender, projecting in posterior and somewhat lateral direction, reaching far behind posterior end of inter-zonal part. Length of cornua almost equalling half the distance from their tips to rostral end of shield. Inner margin of cornua without denticles. Pectoral sinus deep, fairly broad. Inter-zonal part narrow, rather long and high, dorsally with a strong median spine; its posterior breadth contained about two and a half times in maximum breadth of shield. Postero-dorsal portion of inter-zonal part protracted backwards far behind level of postero-lateral angles. Dorsal sensory field rather short and broad, hardly twice as long as broad. Lateral sensory fields reaching backwards to basal parts of cornua. Orbital openings comparatively small, situated rather far in front of middle of length of shield in median line. Narrow independent pineal plate present. Superficial layer of exoskeleton discontinuous. Ornamentation consisting of obtuse tubercles of varying sizes. Mucous canal system not enclosed in exoskeleton.

Holotype. — Cephalic shield (no. A30085) in the Palaeontological Museum, Oslo.

Material. — To this species I refer with certainty only three specimens (Pal. Mus. Oslo nos. A30085, A30086 and A30101); the holotype (no. A30085; pls. 27:2; 28:1; 29—31; 32:1-3; 35:3; 114:1) consists of an incomplete cephalic shield, partly in counterpart, lacking the distal parts of the cornua and most of the dorsal spine; no. A30086 (pl. 33:3) consists of a cephalic shield in a very imperfect state of preservation, much weathered and worn, lacking most of the left half and most of the dorso-median parts, but with the right cornu preserved in its entire length; the very imperfect specimen no. A30101 consists of parts of the dorsal exoskeleton, exposed in ventral view. Besides these specimens one additional specimen (Pal. Mus. Oslo no. A30087), is placed here with some hesitation; it consists of a cephalic shield lacking some of its left postero-lateral parts, the distal parts of the right cornu and of the dorsal spine; it is furthermore somewhat compressed laterally so that the exact shape of its shield is not quite clear.

Description. — The holotype shield has the following dimensions. The length in the median line is 11 cm; the breadth at the level of the anterior end of the pectoral sinus is 12.5 cm. The breadth of the inter-zonal part between the postero-lateral angles is about 5.8 cm. The distance of the postero-lateral angles of the inter-zonal part from the rostral end of the shield is about 9.3 cm, and the distance of the pineal groove from the rostral end of the shield is 4.9 cm. The height of the shield at the posterior end of the inter-zonal part is 5.1 cm. In no. A30086 the inter-zonal breadth is 5 cm and the maximum breadth of the shield, which lies between the tips of the cornua, is estimated at about 15 cm; the distance of the postero-lateral angles from the rostral end of the shield is 9.1 cm and that of the pineal canal from the rostral end of the shield is 4.4 cm. The shield no. A30087, doubtfully placed here, measures 10.9 cm in median length, and the distance of the rostral end from the postero-lateral angles of the inter-zonal part is 9.1 cm and from the pineal groove 4.9 cm; the height of the shield is about 5.7 cm. The shields thus belong to a fairly large species.

Taken as a whole the cephalic shield of this species is moderately broad, with a maximum breadth about one and a third times as great as the length in the median line, and the breadth of the shield at the level of the anterior end of the pectoral sinus is about equal to the median length of the shield; the maximum breadth is furthermore slightly less than the distance of the tip of a cornu from the rostral end of the shield.

The rostral portion of the shield is rather broad and thus the shield decreases forwards only moderately in breadth; the rostral margin is obtusely convex without any trace of a rostral angle. At the transition between the rostral and the lateral margins the margin is rather strongly curved or with slight indication of a very obtuse and rounded angle. The lateral margins, which are very slightly curved, are inclined at an angle of between 20 and 25 degrees to the main axis of the shield. The cornua project in a posterior and slightly lateral direction, and their lateral margins form a direct continuation of those of the main shield.

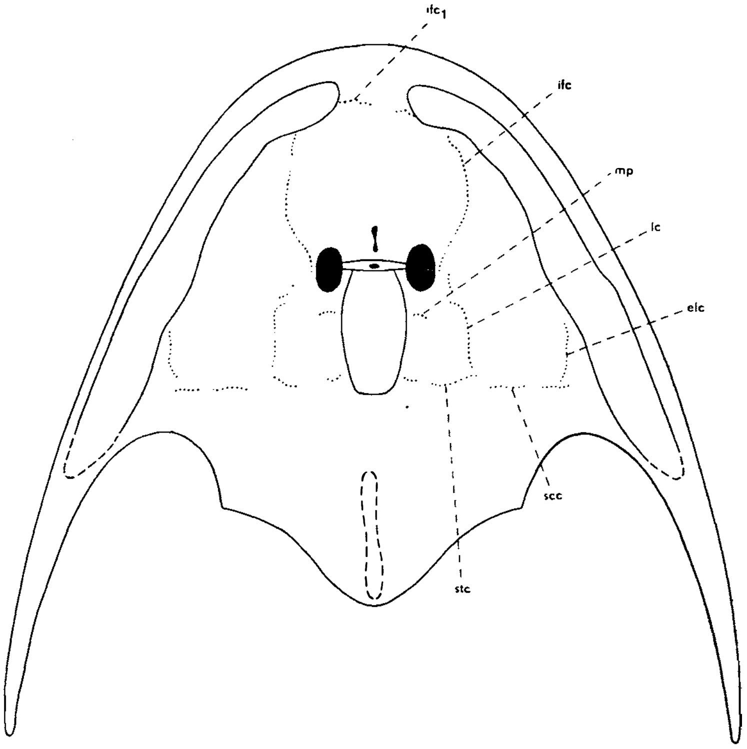


Fig. 51. — *Cephalaspis signata* n. sp. Restoration of the cephalic shield, dorsal view. After Pal. Mus. Oslo nos. A30085—A30086. (The line of short dashes on the inter-zonal part indicates the outline of the upper end of the preserved part of the dorsal spine in cross-section.) ⅔.

elc, extra-lateral sensory line; *ifc,* infraorbital sensory line; *ifc*1, anterior division of the infraorbital sensory line; *lc,* main lateral line; *mp,* anterior transverse sensory line; *scc,* scapular sensory line; *stc,* supratemporal sensory line.

The cornua are very long and rather slender and only very slightly curved; they reach far behind the level of the posterior end of the inter-zonal part. The length of the cornua is contained not much more than twice in the distance of their tips from the rostral end of the shield and about one and a half times in the length of the shield in the median line. The inner borders of the cornua seem to be devoid of denticles although no absolute certainty can be gained on this point as the only cornu which is preserved in its entire length (in no. A30086) is much weathered and abraded. The pectoral sinus are rather deep and fairly broad, somewhat broader in no. A30086 than in the holotype; they are rather uniformly concave. The inter-zonal part is fairly long and narrow and very high; the breadth between the postero-lateral angles constitutes about two-fifths of the maximum breadth of the shield. The maximum height of the inter-zonal part (the dorsal spine excluded), which as usual lies at the posterior end, is only somewhat less than the breadth of the same part. The postero-dorso-median portion of the inter-zonal part is much protracted backwards and its posterior margin is narrowly rounded, forming an obtuse and very indistinct posterior angle; this angle thus reaches backwards far behind the postero-lateral ones. Dorsally the inter-zonal part was very probably provided with a strongly developed median spine, possibly of a similar shape as in *C. corystis* or in *C. hastata;* only the most basal part of the spine is, however, preserved in the holotype: it measures at the basis about 31 mm in length and is about 5 mm broad; its anterior root lies just posteriorly to the posterior border of the dorsal sensory field; in no. A30101 an antero-basal part of the spine is preserved. The dorsal sensory field is comparatively short, not quite twice as long as broad with its maximum breadth somewhat before the middle of its length, and with the lateral margins slightly converging in anterior and posterior direction from that point; the posterior margin is rather obtusely rounded; the anterior margin, which lies immediately behind the pineal groove is abruptly truncated. The distance of the posterior end of the field from the posterior angle of the inter-zonal part is somewhat more than one and a half times as great as the length of the field. The lateral fields are rather narrow in their anterior halves; their most anterior portions are, however, slightly widened; posteriorly they become somewhat broader; behind they reach to the basal parts of the cornua. The distance between the antero-median ends of the two fields is rather small, being only slightly greater than the inter-ocular breadth. The orbital openings, which are small in proportion to the size of the shield, are oval in shape and situated rather far in front of the middle of the length of the shield in the median line. The distance of the orbital openings from the rostral end of the shield is in the holotype and in no. A30087 about equal to that from the pectoral sinus but seems to be somewhat greater in no. A30086. The inter-orbital breadth is somewhat more than twice as great as the transverse diameter of an orbital opening. The orbital openings are surrounded by thick circumorbital ridges and antero-medially to them there are strongly developed antorbital prominences. An independent pineal plate was present in the living animal, its shape and position is indicated by the pineal groove which lies between the middle parts of the orbital openings and which is very narrow, especially in its lateral parts near the orbits. The circumnasal fossa is rather well defined, in the holotype its anterior division forms a triangle-shaped depression; in no. A30087 this depression is roundedly quadrangular in shape.

The outer face of the exoskeleton is ornamented with numerous rounded tubercles of varying sizes, which are rather obtuse in all places, where they have been seen in cross-section: otherwise the tubercles could only be observed from the inner side av the exoskeleton. On the basal parts of the cornua are scattered, comparatively large tubercles, surrounded by numerous small tubercles. The superficial layer and the upper division of the middle layer are discontinuous and present in the tubercles only. The lower division of the middle layer has well developed radiating canals disposed in rather regular, small vascular areas, the average diameter of a vascular area being 1.2 mm. The basal layer is rather thick in the postero-dorsal portion of the inter-zonal part; it contains no regular ringsinus but in its basal parts there are irregular canal-like cavities. The mucous canal system was not enclosed in the exoskeleton but lodged in open grooves, and we can distinguish between fairly wide circum-areal grooves, dividing the outer parts of the exoskeleton into irregular polygonal areas (seen in pls. 28:1; 114:1) and intra-areal grooves, forming a coarse-meshed network within the polygonal areas.

The sensory line system was situated in fairly wide open grooves; these grooves run independently of the circum-areal grooves and pass through the middle of the polygonal areas (pls. 28:1; 114:1). The course of the grooves is indicated in fig. 51; it may only be noted here that there exists a lateral longitudinal groove *(elc)* belonging to the extralateral line.

The endoskeleton is very well ossified in the holotype, in no. A30087 it seems, however, to be rather poorly preserved and in no. A30086 almost nothing of it is observed. Several of the canals of the superficial nerves and vessels are distinguished in the holotype; the canals of the nerves for the lateral sensory fields seem to be disposed as normally in the genus; the canal vls_3 joins most basally the canal vls_4, and the common short trunk, thus formed, opens into the canal *vcl* behind the orbit (pl. 32:3); the canals vls_5 and vls_6 join basally, and also the canals vls_7 and vls_8 unite in their turn before opening into the canal *vcl;* this latter canal thus emits three basal trunks for the dorso-lateral superficial veins. Moreover, in the holotype very much of the inner structure of the shield is displayed and this specimen has repeatedly been mentioned in the chapters on the general anatomy in this paper.

Remarks. — *C. signata* is characterized by its moderately broad and rather high cephalic shield with very long and slender cornua, and a probably very strongly developed dorsal spine. It probably belongs to the same group of species as *C. hastata* (p. 356), *C. ibex* (p. 360), *C. corystis* (p. 352) and *C. isachseni* (Stensiö 1925, p. 253); it has thus many features and i. a. the minute structure of the exoskeleton in common with these species. It differs from them all by the narrow cephalic shield, the broad, obtusely rounded rostral margin and by the very long, almost straight cornua, reaching far behind the posterior end of the main shield.

There is a slight possibility that *C. signata* is the same as *C. spitsbergensis* (Stensiö 1927, p. 276; see also this paper p. 422), but as the holotype of the latter species is very badly preserved no closer comparisons can be made and it thus seems more appropriate to describe the specimens, here united, under a new name. In some respects the species also resembles *C. gracilis* (Stensiö 1927, p. 279) but this species is too imperfectly known as to allow a closer comparison to be made.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the upper parts (the Ben Nevis division).

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, between the First and Second Glaciers ("Tunge"; nos. A30085 and A30101); in a loose slab on the shore (no. A30086); the Second Glacier, in the moraine ("Cephalaspis Moraine"; no. A30087, hesitatingly placed here).

All the specimens were collected during Th. Vogt's expedition in 1928.

30. *Cephalaspis corystis* n. sp.

(Fig. 52; pls. 33:2; 34:2-3.)

Diagnosis. — A rather large *Cephalaspis* species with maximum breadth of cephalic shield about one and a third times as great as length of shield in median line. Shield fairly much narrowing forwards, rostral margin fairly broad, curved without rostral angle. Lateral margins somewhat convex. Cornua moderately long, slender, slightly curved, projecting in posterior and very slightly lateral direction, reaching backwards about as far as posterior end of inter-zonal part. Length of cornua contained about three and a half times in distance of their tips from rostral end of shield. Inner margins of cornua without denticles. Pectoral sinus shallow, of moderate breadth. Inter-zonal part short, very broad, its breadth distinctly greater than half of maximum breadth of shield. Posterior margin with very obtuse angle between posterior and each of postero-lateral angles. Dorsal side of inter-zonal part with high, straight, vertical median spine. Dorsal sensory field elongate, somewhat more than twice as long as broad, with almost parallel lateral margins. Lateral sensory field fairly broad, reaching backwards only to most basal part of cornua. Orbital openings small in proportion to size of shield, situated in front of middle of length of shield in median line. No independent pineal plate present. Exoskeleton ornamented with numerous tubercles of somewhat varying sizes. Superficial layer discontinuous. Mucous canal system not enclosed in exoskeleton.

Holotype. — Cephalic shield (no. A30088) in the Palaeontological Museum, Oslo.

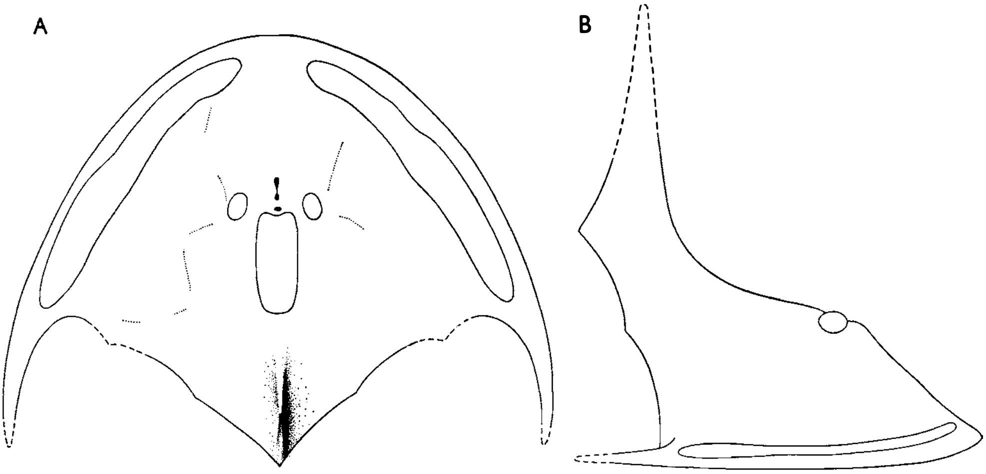


Fig. 52. — *Cephalaspis corystis* n. sp. Restoration of the cephalic shield, A, in dorsal, B, in lateral view. After the holotype (Pal. Mus. Oslo no. A30088). ½.

Material. — Only one specimen (the holotype, Pal. Mus. Oslo no. A30088) is referable to this species; it consists of a fairly complete cephalic shield, in counterpart, lacking the distal part of the dorsal spine and the tips of the cornua; it is somewhat crushed and slightly distorted by pressure in the rock.

Description. — The dimensions of the holotype shield are the following: The length in median line is 11.1 cm; the maximum breadth which lies between the distal parts of the cornua, could not be directly measured, it may, however, be estimated at about 14 cm. The breadth of the inter-zonal part was originally probably about 8.8 cm, but it could not be directly measured in the present state of preservation of the shield. The distance of the tip of the left cornu from the rostral end of the shield is estimated at 11.8 cm. The distance of the pineal foramen from the rostral end of the shield is 4.7 cm. The height of the dorsal spine in its present state is 3.8 cm, but to judge from the shape of its preserved part it seems very probable that it originally was much greater, and the original height is estimated at about 7 cm.

Taken as a whole the cephalic shield is rather broad with a maximum breadth that exceeds the length in the median line about one and a third times; the shield is furthermore characterized by its very broad inter-zonal part, provided with a high vertical dorsal spine.

The shield narrows fairly rapidly forwards and the rostral margin of the cephalic shield is broad and somewhat rounded without any trace of a rostral angle. There are no boundaries between the rostral and the lateral margins and the latter are not very strongly convex. The lateral margins of the main shield merge into those of the cornua without interruption, the whole lateral margins being thus uniformly curved. The cornua, which are very slender and slightly curved, project in a posterior and slightly lateral direction; they extend backwards to about the same level as the posterior end of the inter-zonal part. As most of the right cornu and the tip of the left cornu are missing the actual length of the cornua could not be ascertained: it seems, however, very probable that the real length of the cornua was only very slightly greater than the length of the left cornu in its present condition; they attained thus only a moderate length, which was contained almost three and a half times in the distance of their tips from the rostral end of the shield or about three times in the length of the shield in the median line. The inner margins of the cornua are not provided with any denticles. The pectoral sinus are shallow and not very broad, they seem to be uniformly concave. The interzonal part is short and very broad; its postero-lateral angles are only slightly protruding; its breadth constitutes about three-fifths of the maximum breadth of the shield. The posterior end of the interzonal part extends backwards far behind the postero-lateral corners and the posterior angle thus formed is acute. The height of the inter-zonal part is rather small; it is contained about two and a half times in the breadth of that part. The posterior margin between each postero-lateral and the posterior angle is not uniformly bent but forms a distinct though very obtuse angle somewhat behind the middle of its length. The postero-dorsal portion of the inter-zonal part is provided with a vertical median spine; only the basal part of it is preserved but, to judge from the shape of this part, the spine was probably comparatively very high and straight. The spine seems, however, to be somewhat lower than that in *C. hastata* and *C. ibex;* it is rather long (38 mm) at the basis and tapers rapidly distally, its shape seems thus to have been somewhat similar to that of *C. ibex* but the spine is straightly erect as in *C. hastata* and in *C. doryphorus*. The anterior root of the spine lies just behind the posterior margin of the dorsal sensory field. The sensory fields are rather well developed. The dorsal field is elongate, about twice as long as broad; its lateral borders are almost parallel, only slightly converging most anteriorly between the posterior parts of the orbital openings; the posterior margin is broadly rounded and the anterior one has a rather broad median notch or sinus, in which the pineal foramen is partly situated. The lateral sensory fields are rather broad and slightly broader in their posterior than in their anterior halves; they reach backwards only to the most proximal parts of the cornua but extend rather far antero-medially, and the breadth of the space between them is here about as great as the inter-orbital breadth. The orbital openings are very small in proportion to the size of the shield, they are roundedly oval in shape and surrounded by thick circum-orbital ridges; they are situated at about the same distance from the rostral end of the shield and from the pectoral sinus but much nearer to the rostral than to the posterior end of the shield. The inter-orbital breadth is slightly more than twice as great as the transverse diameter of an orbital opening. The antorbital prominence is well developed. The pineal foramen, which is not situated in an independent pineal plate, lies between the middle parts of the orbital openings. The circum-nasal fossa is rather narrow and well defined; its anterior division is much deeper than the posterior one.

The outer face of the exoskeleton is ornamented with numerous tubercles of somewhat different dimensions, but all of rather small size. On the inner margins of the cornua the tubercles are small and low and somewhat elongated; the shape of the tubercles on the main parts of the shield is almost circular, and in the places where their outer shape has been observed they are rather low and pointed. The superficial layer and the upper division of the middle layer are discontinuous and only present in the tubercles. The lower division of the middle layer is provided with radiating vascular canals of very fine calibres; they are often somewhat irregularly disposed but on the whole form distinct polygonal vascular areas with an average diameter of only 1.4 mm; the ascending vascular canals in the tubercles are well developed as a fine canal plexus. The basal layer contains no ringsinus. The mucous canal system was not enclosed in the exoskeleton but lay entirely in soft tissue outside it and nothing can be said about its development. Several of the grooves of the lateral line system are seen in the shield and the courses of the observed grooves are shown in fig. 52A.

The endoskeleton is rather well ossified but only some parts, e. g. the anterior portion of the roof of the oralo-branchial chamber, are well exposed. Nothing can thus be said about the disposition and the development of the canals for the nerves to the lateral sensory fields nor of any of the dorso-lateral superficial veins.

Remarks. — *C. corystis* is characterized by the size and proportions of its shield, the very broad inter-zonal part with its high dorsal spine, and by the slenderly built cornua, and thereby easily separated from its congeners. It very probable is akin to *C. hastata, C. ibex* (p. 360), *C. signata* (p. 347) and possibly most closely to *C. isachseni* (p. 382 and Stensiö 1927, p. 253), which all possess a strongly developed dorsal spine and a similar development of the exoskeleton. *C. corystis* is the oldest *Cephalaspis* species, representing this peculiar morphological type; it occurs in the lowest known fossiliferous horizon of the Old Red layers in Spitsbergen.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the "Psammosteus" horizon.

Locality. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, E. part (at the top of the ridge), in the "Psammosteus" horizon.

The single specimen was found during Th. Vogt's expedition in 1928.

31. *Cephalaspis hastata* n. sp.

(Fig. 53; pls. 32:4; 33:1; 35:1; 36:2.)

Diagnosis. — A *Cephalaspis* species of medium size with maximum breadth of cephalic shield about one and a half times as great as length of shield in median line. Shield rapidly narrowing forwards. Rostral margin fairly narrow, slightly convex without rostral angle. Lateral margins very slightly curved. Cornua fairly short and rather slender, projecting in postero-lateral direction, reaching somewhat behind posterior end of inter-zonal part; their distal parts very slightly curved backwards. Length of cornua contained about three times in distance of their tips from rostral end of shield. Inner margins of cornua without denticles. Pectoral sinus deep and rather narrow. Breadth of inter-zonal part contained somewhat more than twice in maximum breadth of shield. Inter-zonal part rather long and moderately high, provided with a very high vertical dorsal spine, which gently tapers towards its apex. Dorsal sensory field rather short, about one and a half times as long as broad, with truncated anterior and bluntly rounded posterior margins. Lateral sensory fields reaching backwards over basal parts of cornua. Orbital openings situated nearer to rostral end of shield than to posterior end or to pectoral sinus; of moderate size. Independent pineal plate present. Exoskeleton ornamented with numerous more or less pointed tubercles. Mucous canal system not enclosed in exoskeleton.

Holotype. — Cephalic shield (ENS no. 557).

Material. — The material which can with certainty be placed in this species consists of only one specimen, the holotype (ENS no. 557). In addition to this specimen, however, I place here with hesitation one specimen (Pal. Mus. Oslo no. A30089). The holotype (pls. 35:1; 36:2) consists of a cephalic shield in counterpart, lacking most of its left half. No. A30089 (pls. 32:4; 33:1) consists of a very imperfectly preserved shield, lacking a considerable portion of its lateral parts including the cornua and the distal part of the dorsal spine.

Description. — The holotype has the following dimensions. The length of the shield in the median line is about 63 mm. The maximum breadth of the shield, which very probably lay between the tips of the cornua, could not be measured directly but is estimated to be slightly more than 105 mm. The distance of the tips of the cornua from the rostral end of the shield is estimated at somewhat more than 80 mm. The breadth of the inter-zonal part is about 50 mm and its height at the posterior end (the dorsal spine not included) is about 25 mm. The height of the dorsal spine in its present state of preservation is 46 mm but as the very apex is missing its real height must have been slightly more or about 50 mm. The distance of the pineal groove from

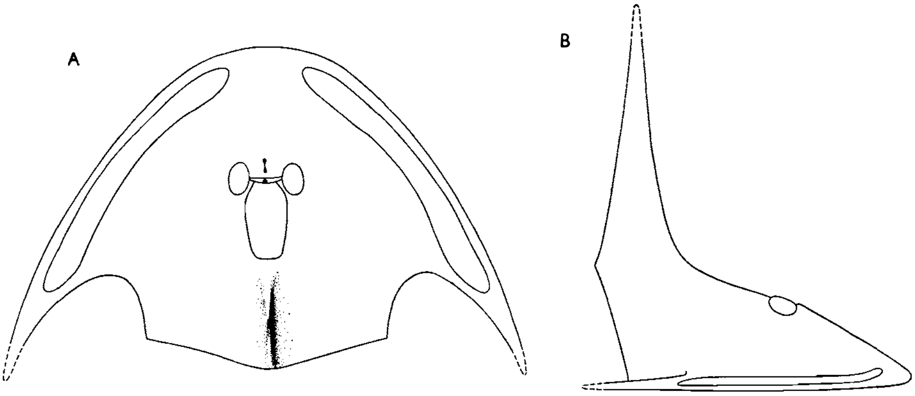


Fig. 53. — *Cephalaspis hastata* n. sp. Restoration of the cephalic shield, A, in dorsal, B, in lateral view. After the holotype (ENS no. 557). ⅔.

the rostral end of the shield is 30 mm. With regard to no. A30089, doubtfully placed here, the length of the shield in the median line is about 67 mm and the distance of the pineal foramen from the rostral end of the shield is 29 mm; this specimen seems thus to agree very well in size with the holotype. On the whole the shields indicate that the species attained only a medium size.

In general shape the shield is fairly low and broad with a maximum breadth that is about one and a half times as great as the length in the median line; the most distinguishing feature of the shield is the very high vertical dorsal spine.

The shield rather rapidly decreases in breadth forwards and the rostral end of the shield is moderately narrow. The rostral margin is obtusely and uniformly rounded without any rostral angle. There seem to be very slight angles at the transition of the rostral margin to the lateral margins, and the rostral margin thus seems to be somewhat better defined than in *C. corystis* and *C. ibex;* as the shield is imperfectly preserved at that place there is, however, some uncertainty about that fact. The lateral margins are very slightly convex. The cornua project in a postero-lateral direction, and their lateral margins form a direct continuation, without any boundaries, of those of the main shield. The cornua taper rather rapidly distally and are on the whole fairly slender; their distal parts are only very slightly bent in a more posterior direction than their proximal parts. The cornua reach somewhat behind the posterior end of the inter-zonal part but as their most distal parts are missing, their real length cannot be determined; it seems likely that they only attained a moderate length, which was contained about three times, or slightly less, in the distance of their tips from the rostral end of the shield or about twice in the length of the shield in the median line. The inner margins of the cornua are devoid of denticles. The pectoral sinus are deep and rather narrow, with a very slight indication of an antero-median corner, and thus slightly asymmetrical. The inter-zonal part is rather long and broad, it narrows only slightly backwards towards its postero-lateral angles, and its breadth constitutes somewhat less than half of the maximum breadth of the shield. The posterior angle of the inter-zonal part, which is very obtuse, reaches only slightly behind the level of the postero-lateral angles. The height of the inter-zonal part (if the dorsal spine is not included) seems to be moderate. Dorsally the inter-zonal part is provided with a very high, straight, median spine; unlike that of *C. ibex* it is almost vertical or only very slightly inclined anteriorly, and its length at the basis is rather small (about 15 mm); it tapers gently and gradually towards its apex. It is probable that the spine attained a height which was about equal to the distance from its anterior root to the rostral end of the shield. The dorsal sensory field is rather small, about one and a half times as long as broad; it is slightly broader in its anterior half than posteriorly, and provided with a bluntly rounded posterior margin; most anteriorly the field narrows towards its anterior transverse margin, which lies immediately behind the pineal groove; it is thus of about the same shape as that of *C. ibex*. The posterior end of the dorsal field lies somewhat in front of the dorsal spine and the length of the intervening space is about half as great as the length of the field; the distance of the posterior end of the field from the posterior end of the inter-zonal part is about one and a half times as great as the length of the field. The lateral sensory fields are moderately broad; they reach backwards only over the proximal parts of the cornua and do not reach the middle of the cornua. The distance between the antero-median parts of the two fields is about twice as great as the inter-orbital breadth. The orbital openings are of a moderate size and oval in shape; they are situated rather far forward on the shield and nearer to the rostral end of the shield than to the posterior end of the inter-zonal part or to the pectoral sinus. The orbital openings lie rather near each other, the inter-orbital breadth is comparatively small and about equal to the transverse diameter of an orbital opening. The circum-orbital ridge as well as the antorbital prominence are well developed. An independent pineal plate was present; its shape and position are indicated by the pineal depression, which is narrow and lies between the middle parts of the orbital openings. The circum-nasal fossa is rather narrow; its anterior semicircular division is deep and well defined along its anterior border.

The outer face of the exoskeleton is ornamented with numerous tubercles, which on the whole are of a rather similar size but which vary somewhat in shape, some of them being rather blunt while others are more pointed. The average distance between two tubercles is 1.2 mm. As the tubercles are situated each above one vascular area, this figure indicates also the average diameter of the vascular areas. The superficial and the outer division of the middle layer are only present in the tubercles but absent in the inter-tubercular spaces. The radiating canals are well developed. The basal layer contains no ringsinus. The mucous canal system was not enclosed in the exoskeleton but lay in the soft tissue outside it, probably in the grooves between the tubercles.

The endoskeleton is well ossified and several of the bone-layers lining it are displayed in the present specimen. It may only be noted here, that the canals for the nerves to the lateral sensory field behave as normally in the genus, and the canals vls_3 and vls_4 join into a very short common trunk, which opens into the postero-lateral corner of the orbit.

With regard to the specimen (no. A30089), doubtfully placed here, some remarks may be allowed. Contrary to what is the case in the holotype the dorsal sensory field has its greatest breadth somewhat posterior to the middle of its length. No independent pineal plate is present. The ornamentation of the outer face of the exoskeleton consists of numerous tubercles which in the region posterior to the orbit seem to be somewhat smaller than in the holotype, and in the inter-zonal part the tubercles are of two different sizes, partly larger ones, situated one over the center of each vascular area (the distance between two such tubercles being about 1.9 mm) and partly smaller ones which surround the larger tubercles. In the anterior parts of the shield (in front of the orbits) the tubercles form small narrow transverse ridges of somewhat different sizes, the larger ones being about 1 mm in transverse length.

Remarks. — *C. hastata* is characterized by the very high, straight, almost vertical dorsal spine and by the general shape of the shield, the cornua and the inter-zonal part. It is very similar to *C. ibex* but differs from this species mainly by the shape of the dorsal spine, and furthermore by its lower shield, with broader rostral margin, deeper pectoral sinus, and shorter dorso-median portion of the inter-zonal part. As, however, these differences seem fairly insignificant, the two species may possibly turn out to be different forms (subspecies or varieties) of one variable species. From the other known *Cephalaspis* species, characterized by a high dorsal spine, it is easily distinguished by the size and the general proportions of its shield and by the shape of the dorsal spine. It is certainly most closely related to *C. ibex* and somewhat more distantly to *C. corystis* (p. 352), *C. isachseni* (p. 382) and *C. signata* (p. 347), but shows no closer affinities to *C. doryphorus* (p. 364) or *C. websteri* (Stensiö 1932, p. 133).

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Anglaspis horizon.

Localities. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Anglaspis horizon (no. 557); the specimen (no. A30089), doubtfully placed here, is found on Mt Ben Nevis, N. W. side, between the First and Second Glaciers ("Tunge").

No. 557 was collected by the ENS expedition in 1939, no. A30089 by Th. Vogt's expedition in 1928.

32. *Cephalaspis ibex* n. sp.

(Fig. 54; pls. 28:2-3; 35:2; 36:1; 37—38.)

Diagnosis. — A *Cephalaspis* species of medium size with high cephalic shield and with maximum breadth of shield probably at least one and a third times as great as length of shield in median line. Shield rapidly narrowing forwards. Rostral margin narrow, sharply rounded without rostral angle. Lateral margins very slightly curved. Cornua projecting in postero-lateral direction, fairly slender and (probably) rather short. Pectoral sinus fairly deep, of moderate breadth. Interzonal part broad, as high as broad, with very high, anteriorly inclined dorsal spine, which is rather long at its basis and tapers rapidly towards the pointed tip. Dorsal sensory field rather small, somewhat less than twice as long as broad, with truncated anterior and posterior margins. Lateral sensory fields reaching backwards over basal parts of cornua. Orbital openings situated nearer to rostral end than to posterior end of shield. Independent pineal plate present. Exoskeleton ornamented with numerous small tubercles, very closely set on anterior border of shield. Mucous canal system not enclosed in exoskeleton.

Holotype. — Cephalic shield (no. A30090) in the Palaeontological Museum, Oslo.

Material. — The material referable to this species comprises two specimens (Pal. Mus. Oslo no. A30090 and ENS no. 558). The holotype (pls. 28:2-3; 36:1; 37—38) consists of a rather completely preserved cephalic shield in counterpart, lacking the distal parts of the cornua and of the dorsal spine, and somewhat distorted by pressure in the rock. The second specimen (pl. 35:2) consists of a cephalic shield preserved in lateral position; it is much compressed laterally and lacks the anterior and lateral parts of the shield including the cornua but exhibits the almost entire dorsal spine. One specimen (ENS no. 559) is placed here with much doubt; it consists of a very imperfectly preserved shield in counterpart, lacking much of its left half and of the dorsomedian portion of the shield as well as the tip of the right cornu.

Description. — The holotype shield has the following dimensions. The length in the median line is about 81 mm; the breadth at the level of the preserved posterior parts of the cornua is estimated at about 92 mm, and it seems very probable that the maximum breadth of the shield, which probably lay between the distal parts of the cornua, was only slightly greater than 100 mm. The distance of the pineal groove

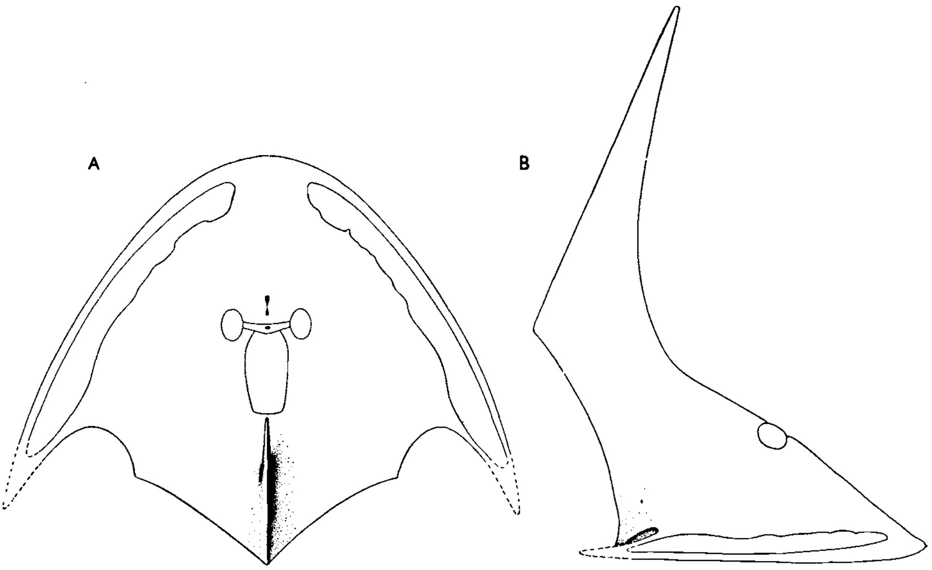


Fig. 54. — *Cephalaspis ibex* n. sp. Restoration of the cephalic shield, A, in dorsal, B, in lateral view. After Pal. Mus. Oslo no. A30090 and ENS no. 558. ⅔.

from the rostral end of the shield is about 35 mm. The breadth of the inter-zonal part between the postero-lateral angles is 26 mm but as this part is much compressed laterally the real breadth must have been much greater and probably at least 40 mm. The maximum height of the main shield, which as usual lies at the posterior end of the inter-zonal part, is estimated at about 40 or 45 mm and is thus comparatively very great. The second shield (no. 558) seems to be slightly greater than the holotype shield but no direct, comparable measurements can be taken; the height of the preserved part of the dorsal spine (along its posterior margin) is 71 mm and the height of the entire spine is estimated at about 80 mm.

The main distinguishing feature of the shield is the powerful dorsal spine, placed on a high inter-zonal part. The shield is fairly broad, its maximum breadth being somewhat (and probably at least one and a third times) greater than the length of the shield in the median line. The shield narrows rather rapidly forwards and its rostral margin is rather narrow and sharply rounded without any rostral angle. Without interruption or with very indistinct and rounded antero-lateral corners the rostral margin passes into the lateral margins. These margins are almost straight or only slightly curved, and on a whole inclined at an angle of about 30 degrees to the main axis of the shield. The cornua are imperfectly preserved, their distal parts are missing, but to judge from the basal parts they project in a postero-lateral direction, their lateral margins forming a direct continuation, without interruption, of those of the main shield. The cornua seem to have been moderately slender and short; their length was probably constituting about two-sevenths or somewhat less of the distance of their tips from the rostral end of the shield, or about one-third of the length of the shield in the median line. Backwards they possibly projected not at all or only slightly behind the level of the posterior end of the inter-zonal part. The inner borders of the cornua are devoid of denticles, at least in their basal parts. The pectoral sinus are rather deep but only moderately broad, uniformly concave without any corners, and somewhat shallower than those of *C. hastata*. The inter-zonal part is rather short, very high, and moderately broad, and slightly decreasing in breadth backwards; its breadth being probably slightly less than half of the maximum breadth of the shield. The height of the inter-zonal part, measured at the posterior end and to the basis of the dorsal spine is rather great and about equal to the breadth of the inter-zonal part; it is thus much greater than in *C. hastata*. The posterior end of the inter-zonal part reaches backwards for some distance behind the postero-lateral angles. The inter-zonal part is provided dorsally with a very high median spine, which is inclined forwards at an angle of about 30 degrees to the perpendicular line; the spine is rather long at its base (about 30 mm in the holotype and about 35 mm in no. 558) but tapers rapidly in its basal part and more gently and gradually in its apical part, thus becoming very slender distally. The height of the spine is considerably greater than the distance of its anterior root (which lies just behind the dorsal sensory field) from the rostral end of the shield but somewhat less than the length of the shield in the median line. Both in the shape and in the direction of the dorsal spine *C. ibex* differs from *C. hastata*. The dorsal sensory field is rather small, about twice as long as broad, roughly rectangular in outline with somewhat convex lateral margins, which are slightly more converging anteriorly than posteriorly; the greatest breadth of the field lies far anteriorly; the anterior margin is slightly concave as it meets the pineal groove, the posterior one is truncated with rounded corners. The distance of the posterior margin of the field from the posterior end of the inter-zonal part is nearly twice as great as the length of the field. The lateral sensory fields are rather narrow, very slightly increasing in breadth backwards with their maximum breadth at the level of the inner end of the pectoral sinus; from that point they taper towards their tips which reach over the basal parts of the cornua. The distance of the antero-lateral ends of the two fields from each other is somewhat more than one and a half times as great at the inter-orbital breadth. The orbital openings, of a moderate size and oval in shape, are situated in front of the middle of the length of the shield in the median line, and their distance from the rostral end of the shield is about equal to that from the pectoral sinus. The inter-orbital breadth is about twice as great as the transverse diameter of an orbital opening. The circum-orbital ridge is strongly developed; the antorbital prominence is well marked but rather small. The pineal groove indicates the presence of a pineal plate in the living animal. The circum-nasal fossa is very deep, but only its anterior part is well defined and rather deep.

The outer parts of the exoskeleton are on the whole not well accessible for investigation and the minute structure of these parts is still rather obscure. The ornamentation consists of comparatively small tubercles which, however, vary somewhat in size and shape, some being small and pointed, others large and blunt. On the anterior border of the shield the ornamentation consists of small blunt, very closely set tubercles, separated from each other by very deep and narrow grooves. The superficial layer as well as probably the outer division of the middle layer are preserved only in the tubercles. The radiating canals are well developed and disposed in distinct fascicles and are of very fine calibres; the average diameter of a vascular area in the middle parts of the shield is in the holotype 1.5 mm. The basal layer contains no ringsinus. The mucous canal system lay very probably outside the exoskeleton, in the soft tissue in the grooves surrounding the tubercles.

The endoskeleton is well ossified and several of the perichondrial bone-layers lining it are exposed. Here only the disposition of some of the canals for the dorso-lateral superficial veins will be mentioned: the canals vls_3 opens directly into the dorso-lateral part of the orbit, the canals vls_5 and vls_6 join into a common trunk which receives the canal vls_4 before opening into the canal *vcl*.

Remarks. — *C. ibex* resembles very much *C. hastata* (and they are perhaps two different forms of one species), but differs by the shape and direction of the dorsal spine as well as by the general shape and proportions of the main shield, and by the much higher inter-zonal part. It reminds somewhat of *C. signata* (p. 347) but is at once distinguished from this species by the size of its shield and the different development of the cornua, and possibly also of the dorsal spine. The species shows more remote affinities to the species *C. corystis* (p. 352) and *C. isachseni* (p. 382 and Stensiö 1927, p. 253).

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Vogti horizon.

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, Northern Part, in the Vogti horizon (no. A30090); the Andrée Glacier, S. half, W. part, in the moraine (no. 558). No. 559, doubtfully placed in this species, was found on Mt Ben Nevis, at the Cliff.

No. A30090 was collected during Th. Vogt's expedition in 1928; nos. 558—559 during the ENS expedition in 1939.

33. *Cephalaspis doryphorus* n. sp.

(Fig. 55; pls. 39; 40:1-3.)

Diagnosis. — A *Cephalaspis* species of rather small size, with maximum breadth of cephalic shield somewhat less than twice as great as length of shield in median line. Shield fairly strongly narrowing forwards. Lateral margins curved. Cornua rather long and stout, projecting in postero-lateral direction, reaching backwards far behind posterior end of inter-zonal part; inner borders with small denticles. Length of cornua contained about three times in distance of their tips from rostral end of shield. Pectoral sinus very shallow, medially very vaguely defined. Inter-zonal part broad and very short, rather high, dorsally with a very high, vertical, rather slender dorsal spine, which tapers gently towards its tip. Postero-dorso-median portion of inter-zonal part somewhat protracted backwards. Dorsal sensory field about twice as long as broad, its lateral sides almost parallel, anterior and posterior margins truncated. Lateral sensory fields extending backwards to basal parts of cornua. Independent pineal plate present. Superficial layer of exoskeleton smooth and continuous. Mucous canal system enclosed in exoskeleton, forming uniform, fine-meshed network.

Holotype. — Cephalic shield (no. A30091) in the Palaeontological Museum, Oslo.

Material. — Only one specimen, the holotype (Pal. Mus. Oslo no. A30091), can be placed in this species; it consists of a fragmentary cephalic shield, lacking the rostral parts and most of its left side as well as the tip of the right cornu.

Description. — As a considerable portion of the rostral part of the shield is missing, the length of the shield in the median line cannot be directly measured; it is, however, estimated at about 30 mm; the distance of the tips of the cornua from the rostral end of the shield is roughly estimated at about 45 mm. The maximum breadth of the shield, which lies between the distal parts of the cornua, is about 55 mm and the breadth of inter-zonal part is 28 mm. The height of the shield which lies between the distal parts of the cornua, is about 55 mm and the breadth of the inter-zonal part is 28 mm. The height of the shield at the posterior end of the shield (the dorsal spine not included) is about 14 mm. It is thus evident that the species attained only a rather small size.

The configuration of the rostral part of the shield is unknown. It is, however, evident that the rostral margin was broad, and it is very probably that it was broadly rounded and possibly without a rostral angle (as is assumed in the restoration, fig. 55A). The lateral margins of the main shield are rather convex and continue into those of the cornua without any interruptions. The cornua which project in a postero-

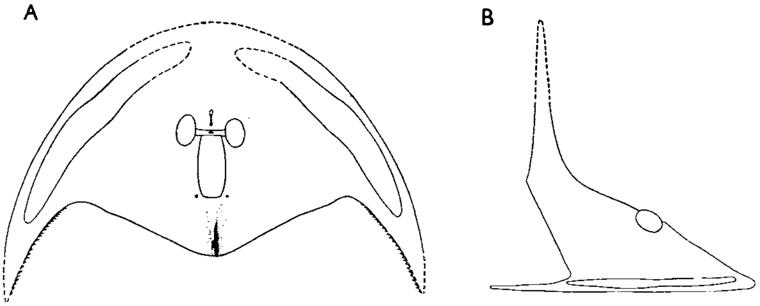


Fig. 55. — *Cephalaspis doryphorus* n. sp. Restoration of the cephalic shield; A, in dorsal, B, in lateral view. After the holotype (Pal. Mus. Oslo no. A30091). Nat. size.

lateral direction, are rather long and reach backwards far beyond the level of the posterior end of the inter-zonal part. The exact length of the cornua could not be ascertained but it seems very probable that it was contained about three times in the distance of the tips of the cornua from the rostral end of the shield and about twice in the median length of the shield. They are flattened dorso-ventrally, and are in their distal parts slightly curved so as to project in a more posterior direction; their inner margins are provided with small, antero-medially directed, slightly curved denticles. In dorsal view the pectoral sinus are ill-defined and very shallow, and have very indistinct boundaries medially; they remind thus somewhat of those in *C. watneliei.* On account of the oblique position of the posterior wall of the zonal part they are, however, slightly deeper and somewhat better defined on the ventral side than on the dorsal side. The inter-zonal part is very short and indistinctly defined from the zonal parts, its postero-lateral angles are very obtuse and rounded. The posterior portion of the inter-zonal part is protracted backwards for some distance behind the postero-lateral angles, and is provided with a very high dorsal median spine, which is rather slender and gently tapering distally (as the spine is broken, its actual length and the shape of its distal parts are unknown); the length of the preserved portion of the dorsal spine is about 10 mm. The dorsal sensory field is elongate and about twice as long as broad, with almost parallel lateral borders; anteriorly and posteriorly the field is truncated with rounded corners; the posterior margin lies closely in front of the basis of the dorsal spine. The distance of the posterior margin of the field from the posterior end of the shield is about equal to the length of the field. The lateral fields are moderately broad, gently narrowing towards their posterior ends which lie on the proximal halves of the cornua. The orbital openings are rather large and oval in shape, their distance from the rostral end of the shield is probably somewhat less than from the posterior end of the inter-zonal part. An independent pineal plate was (very probably) present.

The superficial layer of the exoskeleton is continuous and smooth without any ornamentation; the middle layer is provided with radiating canals, and the basal layer contains no ringsinus. The mucous canal system is enclosed in the exoskeleton and forms a uniform and fine-meshed net-work. With regard to the sensory line system it can be noted that two grooves, belonging to the dorsal sensory line, have been observed.

The endoskeleton is well ossified and several of the internal structures, displayed in the specimen, are recorded in the chapters on the general morphology. Here only some of the superficial canals may be mentioned. The nerve canals for the lateral sensory fields (as far as observed) are developed as normally in the genus. The canal vls_3 opens directly into the dorso-lateral part of the orbit. Each of the other superficial dorso-lateral veins opens into a plexus of rather large anastomosing sinus-like canals, which lies behind the orbital openings.

Remarks. — This species is well characterized by its broad cephalic shield, the very short and broad inter-zonal part and the very high, vertical, slender dorsal spine, and cannot be confused with any other *Cephalaspis* species as yet known. It seems to stand rather isolated systematically and shows no closer connection with the other *Cephalaspis* species provided with a similar high dorsal spine (e. g. *C. corystis, C. ibex).*

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Ctenaspis-horizon.

Locality. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, W. plateau, in the Ctenaspis-horizon.

The only specimen was collected during Th. Vogt's expedition in 1928.

34. *Cephalaspis metopias* n. sp.

(Fig. 56; pl. 41.)

Diagnosis. — A large *Cephalaspis* species with maximum breath of cephalic shield (probably) somewhat less than twice as great as length of shield in median line. Shield moderately narrowing anteriorly, rostral margin very broadly rounded without rostral angle. Lateral margins slightly convex. Cornua well developed, slender, projecting in postero-lateral direction, (exact length unknown), inner margin without denticles. Pectoral sinus broad and shallow. Inter-zonal part broad and comparatively high. Dorsal sensory field with broad truncated anterior margin. Lateral sensory fields reaching backwards to basal parts of cornua, with distinct rounded postero-median dilatation on to zonal part of shield. Orbital openings very small, with well developed circum-orbital ridge. No pineal plate. Exoskeleton ornamented with tubercles

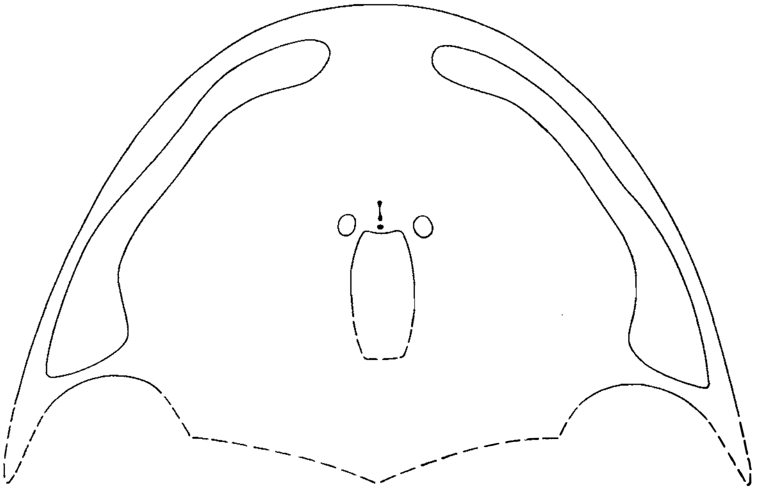


Fig. 56. — *Cephalaspis metopias* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (Pal. Mus. Oslo no. A30092). ½.

of varying size. Basal layer with ringsinus. Polygonal areas small. Mucous canal system partly enclosed in exoskeleton, a portion of it lodged in large circum-areal grooves.

Holotype. — Cephalic shield (no. A30092) in the Palaeontological Museum, Oslo.

Material. — Besides the holotype (Pal. Mus. Oslo no. A30092, pl. 41), which consists of an imperfect cephalic shield in counterpart, lacking a portion of the left half of the shield, the inter-zonal part and the distal half of the right cornu, I have placed here four specimens (Pal. Mus Oslo no. A30093, ENS nos. 560—562). They consist all of anterior shield fragments, the posterior parts including the cornua are wanting. They agree well with the holotype in the observable characteristics but it is of course clear that their assignment to this particular species is not so well founded as is the case in other species.

Owing to the very imperfect state of preservation of all the specimens only very few exact measurements can be taken. If the restoration of the shield in fig. 56 is reasonably correct, the breadth of the shield between the tips of the cornua would be about 20 cm, and the length of the shield in the median line 12.5 cm in the holotype. The distance of the pineal foramen from the rostral end of the shield is 6.4 cm in the holotype, 6.1 cm in no. 560, and 6.5 cm in no. 562. These specimens are thus of about the same size, and that seems also to be the case with nos. 561 and A30093 although no comparable measurements can be taken of these shields. The height of the shield at the posterior half of the dorsal sensory field is about 3.3 cm in the holotype. The species was thus of large size.

On the whole the cephalic shield seems to be very broad and rather short, the maximum breadth, which is assumed to lie between the tips of the cornua, being probably not quite twice as great as the median length of the shield. The shield decreases gently in breadth anteriorly and the rostral margin of the shield is broad, and is broadly and evenly curved; there is no rostral angle. The lateral margins are slightly convex. The cornua project in a postero-lateral direction; to judge from their preserved parts they were rather short and slender but nothing can be said with certainty about their actual length and their shape in the distal parts. Their inner margins, as far as preserved, are devoid of denticles. The pectoral sinus are broad and seem to be very shallow. Very little is preserved of the inter-zonal part yet it is evident that it was broad and rather high; its posterior breadth is assumed to have been about half as great as the maximum breadth of the shield. The dorsal sensory field is preserved only in its anterior half; the lateral margins are slightly curved; the anterior margin is broad and truncated or slightly concave; it lies closely behind the pineal foramen. The lateral sensory fields are peculiarly shaped; they are comparatively narrow in their middle parts, somewhat broader anteriorly; posteriorly, in front of the pectoral sinus, they are much broadened, provided with a roundedly angulate dilatation or short process medially on to the zonal parts, thus reminding somewhat of those in *C. salweyi*. Posteriorly the lateral fields reach backwards only to the most basal parts of the cornua. The distance between the antero-median ends of the two lateral fields is about twice as great as the inter-orbital breadth. The orbital openings are very small in proportion to the size of the shield; they are roundedly oval and situated somewhat nearer to the rostral end of the shield than to the pectoral sinus. The circum-orbital ridge is very broad but probably not particularly high. The inter-orbital breadth is about three times as great as the transverse diameter of an orbital opening. There is no independent pineal plate. The naso-hypophyseal opening is very small; the circum-nasal fossa is rather narrow, rectangular, and anteriorly very deep.

The exoskeleton is imperfectly preserved, and not much can be said with certainty about its minute structure. The outer face of the exoskeleton in the holotype is ornamented with numerous tubercles of varying size, one in each polygonal area, all probably blunt and not very high; it could not be definitely ascertained but seems likely that the superficial layer is continuous and present between the tubercles. In the other specimens the tubercles are of a very inconsiderable size or, along the lateral margins, even absent; the superficial layer is continuous. The middle layer is probably very thin, the radiating vascular canals are present but very delicate. The basal layer is provided with ringsinus. The mucous canal system was lodged in rather narrow circum-areal grooves and thus only partly enclosed in the exoskeleton; of the intra-areal canals nothing has been observed in the holotype; in no. 560 they form a very fine-meshed network enclosed in the exoskeleton. The polygonal areas, formed by circum-areal grooves in the outer parts of the exoskeleton and by ringsinus in the basal layer, and corresponding to the vascular areas, are very small in proportion to the size of the shield; they are of a somewhat varying size and measure on the average 2.2 mm in diameter.

Of the endoskeleton only some faint traces of the canal-layers have been observed in the lateral sensory fields, otherwise it is not preserved or had not been ossified.

Remarks. — Though rather imperfectly known, *C. metopias* seems to constitute a species by itself, distinguished from its congeners and characterized mainly by the large size of its shield, the broadly rounded rostral margin, the peculiar shape of the lateral sensory fields, the small size of the orbital openings and of the polygonal areas in the exoskeleton. In the shape of the lateral sensory fields it is suggestive of *C. salweyi* (Stensiö 1932, p. 90) from the Dittonian of England but otherwise the differences between the two species are evident. In the general shape of its shield *C. metopias* is somewhat similar to *Tegaspis kolleri* (p. 438) but differs by the configuration of its shield and by the development of the sensory fields. In the feature just mentioned *C. metopias* is suggestive of *C? pedata* (p. 375) but the shape of the lateral fields is different, and the pectoral sinus are narrower and the inter-zonal part broader.

C. metopias is placed in the genus *Cephalaspis* although nothing is known of its internal characters and the shape of the lateral sensory fields is rather unfamiliar in the genus; the reference of the species to this genus is thus (as is the case with many other species) only provisional.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Benneviaspis horizon.

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, W. Plateau, in the Benneviaspis horizon (nos. A30092—A30093); the Second Glacier, in the moraine (no. 562); the Andrée Glacier, S. half, W. part, in the moraine (nos. 560—561).

The holotype (no. A30092) and no. A30093 were collected by Th. Vogt's expedition in 1928; the other specimens (nos. 560—562) by the ENS expedition in 1939.

35. *Cephalaspis pinnifera* n. sp.

(Fig. 57; pls. 42; 43:2; 44:2.)

1932. "*Cephalaspis*-like species from Spitsbergen", Stensiö, p. 67 (see also pp. 59, 88); fig. 22.

Diagnosis. — A *Cephalaspis* species of large size with maximum breadth of cephalic shield about one and a half times as great as length of shield in median line. Shield gently narrowing forwards. Rostral margin rather broad, curved without rostral angle. Lateral margins somewhat convex. Cornua robust and rather long, very slightly curved, their length contained somewhat less than three times in distance of their tips from rostral end of shield; projecting in posterior and somewhat lateral direction; reaching behind posterior end of shield. Inner margins of cornua without denticles. Pectoral sinus broad and fairly deep. Inter-zonal part short, rather high, its breadth contained somewhat more than twice in maximum breadth of shield; dorsally with low median spine. Dorsal sensory field rather short and broad, truncated anteriorly and posteriorly. Lateral sensory fields extending very far backwards, ending near tips of cornua. Exoskeleton probably without ornamentation; superficial layer continuous; basal layer with ringsinus. Mucous canal system differentiated into circum-areal and intra-areal canals. Polygonal areas small. Trunk with high dorsal crest.

Holotype. — Incomplete cephalic shield with associated trunk (no. A30096) in the Palaeontological Museum, Oslo.

Material. — Besides the holotype, I refer to this species five cephalic shields (Pal. Mus. Oslo nos. A30094—A30095, A30097, ENS nos. 563—564). The holotype (no. A30096, pls. 42; 43:2; Stensiö 1932, fig. 22) consists of an incompletely preserved and somewhat distorted cephalic shield, lacking a rostral portion and the tips of the cornua, and associated with the shield, an incomplete trunk, wanting the caudal part including the second dorsal fin; the pectoral fins are also lacking. No. A30095 (pl. 44:2) consists of an imperfect cephalic shield, partly in counterpart, lacking the rostral and lateral margins; no. A30097 consists mainly of the dorsal exoskeleton of the incomplete left half of a cephalic shield exposed in ventral view, no. A30094 likewise of the dorsal exoskeleton of the central and postero-median parts of the shield; no. 563 consists of the central and inter-zonal parts of a cephalic shield, and no. 564 of a very fragmentary shield, partly in counterpart, wanting i. a. most of the left, the anterior and the posterior parts.

Description. — As the shields are incomplete in several respects only a few measurements can be taken. The breadth between the distal parts of the cornua in the holotype is about 14.5 cm but as the left side of the shield is much distorted the original breadth is estimated to have been about 17 cm; in no. A30095 the same distance

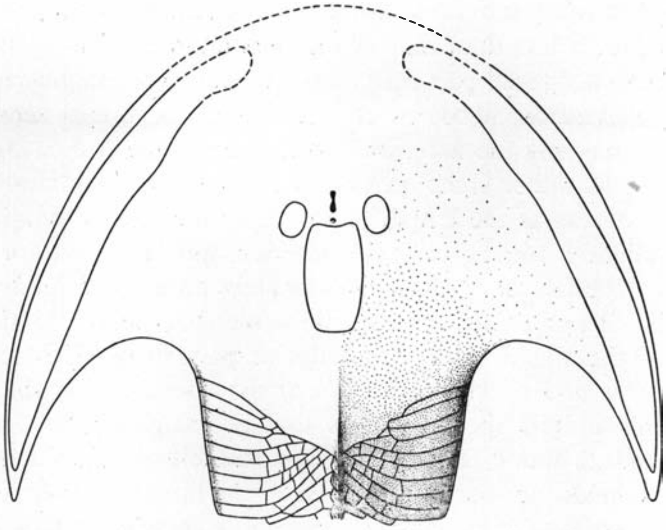


Fig. 57. — *Cephalaspis pinnifera* n. sp. Restoration of the cephalic shield and the anterior part of the trunk in dorsal view. Mainly after the holotype (Pal. Mus. Oslo no. A30096). ½.

is 18 cm. The distance of the pineal foramen from the posterior end of the shield is 6.2 cm in the holotype, in no. A30095 7.2 cm, and in no. 563 it cannot be exactly measured but is probably 6.4 cm. The breadth of the inter-zonal part posteriorly is 7 cm in no. A30095, 7.4 cm in no. 563, and is estimated to be about 7.3 cm in the holotype. The height of the inter-zonal part near its posterior end is 5.3 cm in no. A30095. As seen from the size of the shields, the species must have been of a large size.

The cephalic shield is fairly broad, its maximum breadth which lies near the posterior ends of the cornua, is about one and a half times as great as the length of the shield in the median line. The shield is decreasing in width, but not very rapidly, towards its anterior end. The rostral margin, which is fairly well preserved only in no. A30097, is rather broad and curved; there seems to be no rostral angle developed nor are there any antero-lateral corners at the transition between the rostral and the lateral margins. The lateral margins are somewhat convex. The cornua are rather robust and fairly long; their length constitutes somewhat more than one-third of the distance of their tips from the rostral end of the shield. They project in a posterior and somewhat lateral direction and reach farther backwards than the posterior end of the inter-zonal part. The outer and the inner margins of the cornua are slightly curved; the inner margins have no denticles. The pectoral sinus are broad and moderately deep, they are slightly asymmetrical but there are no antero-median corners. The inter-zonal part is short, moderately narrow and fairly high; its breadth between the postero-lateral corners is less than half of the maximum breadth of the shield. Dorsally the inter-zonal part has a low median spine, slightly increasing in height backwards; it begins closely behind the dorsal sensory field and ends in meeting the anterior dorsal scute of the trunk. The dorsal sensory field is rather short and broad; its breadth is somewhat more than half as great as the length of the field; the lateral margins of the field are slightly convex and the anterior and the posterior margins truncated. The lateral fields are moderadely broad and gently tapering backwards. Their posterior parts lie somewhat nearer to the lateral margins of the shield than their anterior parts; the fields reach very far backwards and nearly to the tips of the cornua. The shape of the lateral fields in this species recalls that of many of the *Cephalaspis* species from the Wood Bay series. The exoskeletal plates, which cover the sensory fields, are partly preserved in the holotype, they are irregularly polygonal in shape and in general somewhat larger than the polygonal areas of the shield. The orbital openings, which are comparatively small and roundedly oval in shape, are situated about midway between the rostral and the posterior ends of the shield or slightly nearer to the rostral end. The distance between the orbital openings is about twice as great as the transverse diameter of an orbital opening or (in nos. 563, 564) somewhat more. In nos. 564 and A30094 there is a very narrow pineal fissure indicating the possible presence of a pineal plate in the living animal; in the other specimens the pineal fissure is obliterated and there was certainly no pineal plate. The naso-hypophyseal opening has the normal development with three divisions, the posterior one lying on a distinct elevation, the anterior one in a rounded, fairly deep, anterior depression of the circum-nasal fossa. This fossa is on the whole rather well defined and equilaterally triangular in shape.

The exoskeleton, particularly its outer parts, is not easily accessible for observation. The outer face of the exoskeleton seems to be quite smooth, no kind of ornamentation has been observed. The superficial layer forms a continuous covering to the middle layer, interrupted only by the grooves of the mucous canal system. The radiating canals are of a very delicate calibre and not disposed in distinct bundles. In the basal layer there are ringsinus, at least in the inter-zonal part (observed areal grooves and very minute intra-areal canals which latter form a fine-meshed network in the intra-areal spaces. In no. A30094 the in no. 563). The mucous canal system consists of fairly large circum-circum-areal grooves near the postero-lateral angle of the inter-zonal part are irregular and somewhat subdivided by secondary canals. The polygonal areas are in general rather small; in no. A30094 on each side of the naso-hypophyseal opening they are very small but there is a very large area of this kind enclosing the antorbital prominence; in the middle parts of the shield in no. A30095 the polygonal areas are on the average 2.5 mm in diameter, and on the inter-zonal part in the holotype 2.3 mm.

The grooves of the sensory line system are developed as short dashes, each within a polygonal area. The grooves of the main lateral line and of the infraorbital line are observed in no. A30094.

The endoskeleton seems to have been rather slightly ossified, parts of the internal layer, the orbital layer and layers lining the post-branchial wall are seen; the superficial canal layers are very imperfectly preserved. The principal canals seem to be disposed as in the majority of the *Cephalaspis* species, the canal sel_1 dividing into two branches just antero-laterally to the orbits and the canal vls_3 entering the orbit in its postero-lateral part, but as to the rest, the courses of the canals are very obscure and no further details can be observed.

A major part of the trunk is present in situ and attached to the cephalic shield. The right half of the trunk is fairly well preserved and exposed, whereas the left half is much crushed and distorted. Anteriorly the trunk must have been roughly triangular in cross-section just like the posterior portion of the inter-zonal part of the cephalic shield. The most characteristic feature of the species is the peculiar shape of the dorsal crest. The crest is, however, very poorly preserved, and its structure and exact shape cannot be fully ascertained as it is partly preserved as an imperfect impression of its left side and its most antero-dorsal parts are lacking. It is, however, probable that the crest begins as a low ridge immediately behind the dorsal spine of the inter-zonal part of the cephalic shield at the level of that dorso-lateral scale-row, which corresponds to the 10th lateral scale-row, and extends backwards over 19 scale-rows. At least in its middle and posterior parts it is very high compared with the dorsal crest, known in other *Cephalaspis* species; a major part, at least, of this high division of the crest consists of a single scute. The posterior end of the crest is well defined, and behind it is a normally developed dorsal ridge scale, dorsally to the dorso-lateral scales, which correspond to the 29th row of lateral scales. Nothing is known of the posterior dorsal fin, but to judge from the irregularly disposed posterior dorso-lateral scales, there really was a posterior dorsal fin developed dorsally to them (cf. the conditions in *Hemicyclaspis)* which must then have been situated rather far anteriorly and at only a slight distance behind the dorsal crest. Behind the dorsal crest there are preserved three dorsal ridge-scales. With regard to the rest of the squamation of the trunk, we find that it is developed essentially as in the other few *Cephalaspis* species known in this respect and in *Hemicyclaspis*. The dorso-lateral scales are, however, subdivided into several rectangular plates, four or five, occasionally six in each transverse row and this subdivision seems, at least partly, to be a primary condition and not due to fractures arisen during fossilization. The first four lateral scale-rows have no distinct corresponding rows of dorso-lateral scales. The lateral scales are disposed in 39 transverse rows, each consisting of one high scale; the height of the scales is decreasing backwards. Of the ventro-lateral scales there are at least 37 transverse rows, each with one scale; the posterior scales are of about the same height as the anterior ones; in their ventral parts the scales are bent somewhat ventro-medially but there is no distinct ventro-lateral ridge and the scales extend seemingly only very slightly on to the ventral face of the trunk.

Remarks. — As seen from the description given above, *C. pinnifera* is in the first place distinguished by the structure of its trunk. With regard to the shape of its cephalic shield the species is not particularly well characterized. It differs from its congeners by the general shape of the shield, the rather stout posteriorly directed cornua, and by the shape of the sensory fields. In this latter respect it is very suggestive of some of the *Cephalaspis* species from the Wood Bay series. On the whole it ressembles especially *C. moy-thomasi* (p. 396), but the shield is larger and broader, the cornua shorter, the inter-zonal part has a dorsal median spine, etc. It also reminds of *C. lanternaria* (p. 416) and *C. gigas* (p. 411) but is smaller and narrower and the rostral part of the shield and the cornua are differently shaped.

The species (or more exactly the specimen no. A30096) has been mentioned and figured by Stensiö (1932, pp. 59, 67, 88; fig. 22) on account of its dorsal crest, which Stensiö interpreted as a structure very different from that, otherwise known in the genus *Cephalaspis*. He thought that the species therefore could not be placed in this genus but that a new genus must be erected for it (Stensiö 1932, p. 88). As here interpreted (p. 233) the dorsal crest is, however, essentially of the same construction as in the other species of *Cephalaspis*. *C. pinnifera* does not in any (known) way differ considerably from the rest of the *Cephalaspis* species, and must thus be referred to this genus.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the upper part (the Ben Nevis division; ? the Benneviaspis horizon).

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, without indication of the exact locality (no. A30096), between the First and Second Glaciers ("Tunge"; nos. A30094—A30095, A30097; the layers in this locality possibly belong to the Benneviaspis horizon, see Kiær & Heintz 1935, p. 15); the Andrée Glacier, S. half, W. part, in the moraine (nos. 563—564).

The specimens nos. A30094—A30097 were collected during Th. Vogt's expedition in 1928 (no. A30096 by L. Størmer), the others (nos. 563—564) during the ENS Spitsbergen expedition in 1939.

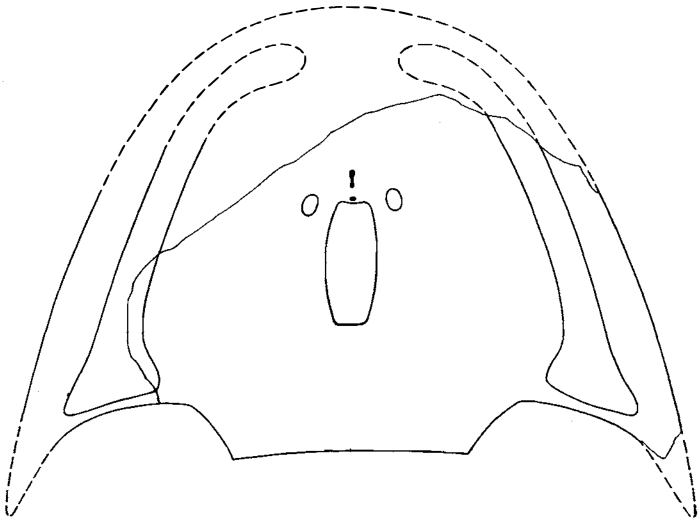


Fig. 58. — *Cephalaspis? pedata* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (Pal. Mus. Oslo no. A21501). ½.

36. *Cephalaspis ? pedata* n. sp.

(Fig. 58; pls. 45; 68:1.)

Diagnosis. — A possible *Cephalaspis* species of large size with maximum breadth of cephalic shield (probably) about one and a half times as great as length of shield in median line. Shield slowly narrowing forwards. Rostral margin very broad. Lateral margins very slightly curved. Cornua projecting in posterior and somewhat lateral direction. Pectoral sinus rather shallow and very broad. Inter-zonal part fairly narrow, rather high, moderately long; dorso-median portion not protracted backwards behind level of postero-lateral angles; dorsally with low median ridge. Dorsal sensory field about twice as long as broad. Lateral sensory fields placed rather far from lateral margin of shield, reaching backwards to most basal parts of cornua, with rather strong triangular process postero-medially. Orbital openings very small; circum-orbital ridge broad. No pineal plate. Exoskeleton ornamented with low blunt tubercles. Superficial layer (probably) continuous. No ringsinus. Mucous canal system partly enclosed in exoskeleton, portions of it lodged in circum-areal grooves, these often subdivided so as to form a coarse network of grooves.

Holotype. — Cephalic shield (no. A21501) in the Palaeontological Museum, Oslo.

Material. — To this species I refer the holotype (Pal. Mus. Oslo no. A21501) only. It consists of an imperfectly preserved cephalic shield in counterpart, lacking most of its anterior and left parts and the distal part of the right cornu.

Description. — As the material of the species is imperfect, the following description must of course be very incomplete. Very few exact measurements can be taken. The breadth of the inter-zonal part between its postero-lateral angles is 6.2 cm, the distance of the pineal foramen from the posterior end of the shield is 6.7 cm and the distance of the orbits from the pectoral sinus is 5.7 cm and 5.9 cm, respectively; the height of the inter-zonal part posteriorly is about 4 cm. On the assumption that the restoration of the shield given in fig. 58 is fairly correct, the maximum breadth of the shield is about 18 cm and the length of the shield in the median line is about 11.5 cm. It is evident that the shield belonged to a large species.

As restored, the shield would be about one and a half times as broad as long. The rostral margin is unknown; to judge from what is preserved of the lateral margins, these are only very slightly curved and converge somewhat anteriorly, and it thus seems probable that the rostral margin was very broad. Only the basal part of the right cornu is preserved, it is flattened dorso-ventrally. On the basis of the preserved part the cornua have been restored as being rather rapidly decreasing in breadth backwards and fairly short; they project in a postero-lateral direction. The pectoral sinus are very broad and rather shallow, somewhat asymmetrical and with a distinct antero-median corner. The inter-zonal part is moderately long and rapidly decreasing in breadth backwards, being remarkably narrow between the postero-lateral angles. It is fairly high and the height at its posterior end is about two-thirds of its posterior breadth. Dorsally the inter-zonal part is provided with a low median ridge, which is slightly increasing in height towards its posterior end; the anterior end of the ridge lies at some distance behind the dorsal sensory field. The dorso-postero-median end of the inter-zonal part does not reach backwards behind the postero-lateral angles; the posterior angle thus is about 180 degrees (viewed from above). The dorsal sensory field is rather narrow and about twice as long as broad, with slightly curved lateral margins and with the anterior and posterior margins truncated. The distance of its posterior margin from the posterior end of the shield is about equal to the length of the field. The lateral sensory fields are placed rather far medially on the shield; there is thus a broad intervening space between their lateral borders and the lateral margins of the shield. They are directed posteriorly towards the pectoral sinus, reach postero-laterally only to the most basal parts of the cornua, and are postero-medially provided with a distinct triangular extension, or, in other words, the lateral sensory fields are posteriorly provided with a rather long and narrow postero-lateral and a somewhat shorter and broader postero-median process. The orbital openings are, as in *C. metopias,* very small in proportion to the size of the shield, they are roundedly oval in shape and surrounded by a broad and rather high circum-orbital ridge. The inter-orbital breadth is almost four times as great as the transverse diameter of an orbital opening. There is no independent pineal plate. The naso-hypophyseal opening is rather small. The circum-nasal fossa is rather well defined, triangular and not particularly deep anteriorly.

The exoskeleton is rather badly preserved. It is ornamented with tubercles, which seem to be blunt-ended and rather low. The superficial layer is present in the tubercles and also very probably in the inter-tubercular spaces between the grooves of the mucous canal system. Very little is seen of the middle layer where the radiating canals are very delicate. In the main parts of the shield no ringsinus are found but in the most posterior portion of the inter-zonal part there are some irregular grooves on the ventral face of the exoskeleton, possibly corresponding to the real ringsinus in other species. The mucous canal system is partly enclosed in the exoskeleton, partly were the mucous canals lodged in broad anastomosing grooves, probably corresponding to the circum-areal grooves in other species, but the areas which they are encircling are very varying in size and their relation to the vascular canal system is not clear. The grooves are in some places simple, in others subdivided by ridges into a wide-meshed network (pl. 68:1), slightly suggestive of that caused by the modified mucous canals in *C. powriei* (Stensiö 1932, fig. 5E, F). Between these grooves the rest of the mucous canal system forms a very fine-meshed plexus, enclosed in the exoskeleton.

Of the sensory line system grooves of the main lateral line and of the infraorbital line are seen; the grooves are situated within the large grooves for the mucous canal system (pl. 68:1).

The endoskeleton seems to have been ossified to a slight degree only, and only some of the most superficial canals for some vessels are observed. Thus nothing can be said of the disposition of the first nerve canal for the lateral sensory field or of the canals for the dorso-lateral superficial veins.

Remarks. — *C? pedata* is mainly characterized by the shape and disposition of its lateral sensory fields, the very broad pectoral sinus and the fairly narrow inter-zonal part (but, as appears from the preceding description, many important details are unknown). It is somewhat similar to *C. metopias* (p. 366) but differs by its narrower shield, broader pectoral sinus, and the shape of the lateral sensory fields. It is also similar in many respects to the genus *Tegaspis* and with regard to the shape of the lateral sensory fields it takes an intermediate position between this genus and the genus *Cephalaspis*. It is by no means proved that it really belongs to this latter genus but for the present and while awaiting better preserved material, which will make clear i. a. the internal characteristics, I place the species provisionally in *Cephalaspis*.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the upper parts (the Ben Nevis division).

Locality. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, N. Plateau (300 m).

The single specimen was collected by Th. Vogt's expedition in 1928.

B. Species from the Wood Bay series (spp. 37—49).

37. *Cephalaspis jarviki* n. sp.

(Fig. 59; pl. 46:2.)

Diagnosis. — A large *Cephalaspis* species with maximum breadth of cephalic shield somewhat greater than length of shield in median line. Rostral margin rather narrow, convex without rostral angle. Lateral margins curved. Cornua rather slender, projecting in posterior direction and reaching somewhat behind posterior end of shield, slightly curved inwards; their length constituting about one-third of distance of their tips from rostral end of shield. Inner margins of cornua without denticles. Pectoral sinus well defined, of moderate depth and breadth. Inter-zonal part rather short; its breadth contained slightly more than twice in maximum breadth of shield; posterior angle protracted behind postero-lateral angles; dorsally with long, low median ridge, continuing backwards in rather long, much inclined dorsal spine. Dorsal sensory field broad and short, length only slightly exceeding maximum breadth, anterior and posterior margins truncated. Lateral sensory fields extending backwards to proximal parts of cornua. Orbital openings small, lying far apart, situated somewhat in front of middle of length of shield in median line. No pineal plate. Exoskeleton ornamented with small closely set tubercles.

Holotype. — Cephalic shield (ENS no. 565).

Material. — The material which can be referred to this species consists of two specimens (ENS no. 565—566). The holotype (no. 565, pl. 46:2) is represented by an imperfect cephalic shield, consisting mainly of the dorsal exoskeleton exposed in ventral view, and lacking some of the anterior parts and the tips of the cornua; it is furthermore somewhat crushed, flattened and distorted by pressure in the rock. No. 566 consists likewise of the dorsal exoskeleton of a fragmentary left half of a cephalic shield, exposed in ventral view.

Description. — Owing to the imperfect state of preservation of the holotype very few exact measurements can be taken. The length of the shield in the median line is estimated at about 14 cm, and the maximum breadth of the shield, which lies across the basal parts of the cornua amounts to 16.8 cm. The breadth of the inter-zonal part between the postero-lateral angles is about 7.5 cm. The distance of the pineal

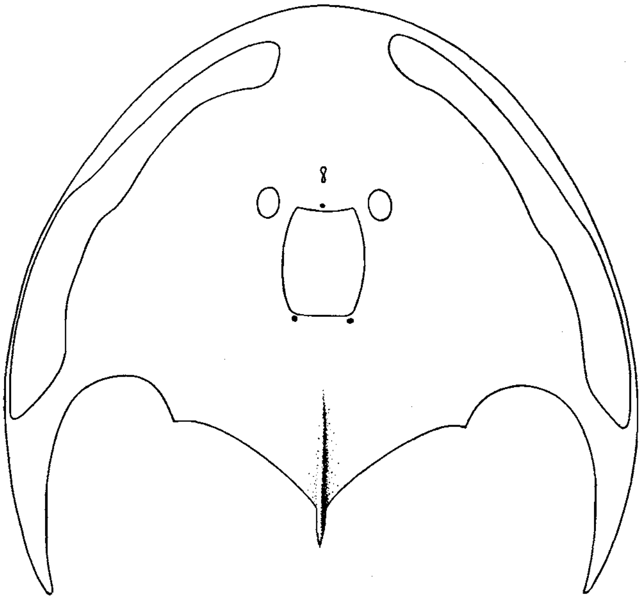


Fig. 59. — *Cephalaspis jarviki* n. sp. Restoration of the cephalic shield, dorsal view. Mainly after the holotype (ENS no. 565). ½.

foramen from the posterior angle of the inter-zonal part is 7.3 cm. The second specimen (no. 566) assigned to this species is of about the same size as the type specimen; no direct measurements can be taken except the distance of the tip of the cornu from the rostral end of the shield, which amounts to 14.6 cm.

Taken as a whole, the cephalic shield is quite large and of moderate breadth; the maximum breadth is only somewhat or about one and one fourth times greater than the length of the shield in the median line (the dorsal spine not included). The rostral margin is not preserved in the holotype but it is evident that it was rather narrow; in the second specimen is seen that it is rather convex and uniformly curved without any rostral angle. The rostral margin merges without interruption into the lateral margin of each side, there are thus no antero-lateral angles. The lateral margins are uniformly and fairly strongly convex. The cornua, which issue in a straight posterior direction, extend to a point somewhat behind the level of the posterior end of the dorsal spine and are thus fairly long, their length being contained nearly three times in the distance of the tips of the cornua from the rostral end of the shield. The cornua are furthermore rather slender, flattened dorso-ventrally, in their distal parts somewhat medially curved, and their inner borders are devoid of denticles. The pectoral sinus are well developed, moderately broad and deep; in the holotype they seem to be uniformly concave, in no. 566, however, there is a distinct antero-median corner. The inter-zonal part of the shield is rather short; its breadth between the postero-lateral angles constitutes slightly less than half of the maximum breadth of the shield. The postero-dorso-median portion of the inter-zonal part is protracted backwards and the posterior angle is rather acute and lies somewhat behind the postero-lateral angles. Dorsally the inter-zonal part is provided with a long, low median ridge which begins somewhat behind the dorsal sensory field and which gradually rises posteriorly and is transformed into an almost horizontal, and very slender dorsal spine, which projects behind the posterior angle of the main inter-zonal part. The dorsal sensory field is broad and short, with a length that only slightly exceeds its breadth; the lateral margins are slightly curved, the posterior margin is abruptly truncated, and the anterior margin, which lies closely behind the pineal foramen is only very little concave; the field ends posteriorly slightly in front of the openings for the ductus endolymphatici. The distance of the posterior margin of the field from the posterior angle of the inter-zonal part is about twice as great as the length of the field. The lateral sensory fields reach backwards only over the basal parts of the cornua; they are rather narrow in their anterior half, distinctly broader in their posterior half, and the broadest part lies somewhat in front of the posterior end. In their anterior part the lateral fields lie at some distance from the lateral borders of the shield but turn laterally at about the middle of the length of the fields and lie close to those borders. The distance of the antero-median ends of the two fields is slightly greater than the inter-orbital breadth. The orbital openings are small in proportion to the size of the shield, roundedly oval in shape, and lie rather far from each other; the distance of the openings from the rostral end of the shield is distinctly smaller than their distance from the posterior angle of the inter-zonal part. The circum-orbital ridge is high but rather narrow. The antorbital prominences which lie antero-medially to the orbital openings, are well developed but blunt and not very high. There is no pineal plate. Only the posterior and part of the middle division of the naso-hypophyseal opening are preserved and lie on the anterior slope of a small nasal elevation; it is evident that the entire naso-hypophyseal opening was very small. The circum-nasal fossa is rather deep and narrow.

The exoskeleton is imperfectly preserved. It must be noted that it is differently developed in the holotype and in no. 566. In the former the superficial layer is present only in the very small rounded and closely set tubercles, which constitute the ornamentation of the outer face of the exoskeleton. On the cornua the tubercles are elongate in shape. The radiating canals are extremely fine. The basal layer contains no ringsinus. The mucous canal system was not enclosed in the exoskeleton but probably situated in the open grooves between the tubercles, and was in this case not differentiated into circum-areal and intra-areal canals. With regard to the second specimen nothing can be said about the superficial layer and its ornamentation; it is, however, seen that the outer parts of the exoskeleton are subdivided into small polygonal areas by the rather wide circum-areal grooves of the mucous canal system. These polygonal areas are observed in the main parts of the shield but not on the inter-zonal part. The average diameter of the areas in the central parts of the shield is 2 mm. On the lateral border, between the lateral sensory field and the very margin of the shield, the polygonal areas are, however, much smaller and somewhat elongated, recalling those in *C. producta*.

Almost nothing is preserved of the endoskeleton; only fragments of the external layer of the inter-zonal endoskeleton are seen in the holotype as well as some canal layers in the lateral sensory fields.

Remarks. — *C. jarviki* is characterized by its rather narrow shield, the shape of the rather slender cornua and of the dorsal spine as well as that of the dorsal sensory field. The shield is of a type which is more common in the Red Bay series than in the Wood Bay series. In the general shape of its shield this species reminds somewhat of *C. watsoni* (Stensiö 1932, p. 137) and particularly of *C. excellens* (p. 308); from both of them *C. jarviki* differs mainly by the larger size of its shield, by the absence of denticles on the cornua, and the non-development of an independent pineal plate; from *C. watsoni* it differs furthermore by the broader anterior part of the shield, the more posteriorly directed cornua, the shallower pectoral sinus, and by the shape of the dorsal sensory field, and from *C. excellens* by the shape of the inter-zonal part, and by the position of the dorsal sensory field as well as by the ornamentation of the exoskeleton, etc.

The second specimen (no. 566) placed in this species agrees very well with the holotype in the general features displayed in the preserved parts of the shield; it differs, however, by the development of the exoskeleton and it might turn out in the future when the species is better known to be sufficiently different from the holotype so as to represent a distinct variety or subspecies.

C. jarviki is named after my esteemed friend Dr. Erik Jarvik, Stockholm, the well-known expert on Devonian vertebrates, who was a member of the ENS expedition to Spitsbergen and who has collected many of the Cephalaspids treated in this paper.

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, the lower part of the C. Kjeldsen division.

Locality. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier (nos. 565—566).

The two specimens were collected during the ENS expedition in 1939.

38. *Cephalaspis isachseni* Stensiö.

1927. *Cephalaspis isachseni,* Stensiö, p. 253; fig. 57; pl. 3.

Diagnosis. — A *Cephalaspis* species of fairly small size with maximum breadth of cephalic shield somewhat greater than length of shield in median line. Shield narrowing anteriorly, rostral margin sharply rounded without rostral angle. Lateral margins slightly curved. Cornua long and slender, projecting in posterior direction and reaching far behind posterior angle of inter-zonal part; length of cornua contained about two and a half times in distance of their tips from rostral end of shield. Cornua somewhat curved inwards, inner margin without denticles. Pectoral sinus broad and shallow. Inter-zonal part moderately broad and short, provided with a high, almost vertical dorsal spine. Dorsal sensory field about two and a half times as long as broad, anterior and posterior margins truncated. Lateral sensory fields reaching backwards to most basal part of cornua. Orbital openings situated much nearer to rostral than to posterior end of shield. Exoskeleton ornamented with numerous tubercles.

Holotype. — Cephalic shield (no. 4) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 253).

Material. — A very badly preserved specimen (ENS no. 567) is at hand; it consists of the flattened central and lateral parts of the shield including the basal portion of the dorsal spine.

Remarks. — Owing to the imperfect state of preservation the specimen does not contribute anything towards a better knowledge of the species and is in fact placed in this species with a slight hesitation.

In the general shape of its shield, *C. isachseni* shows no close resemblance to any of the other species from the Wood Bay series but rather to some of the species from the Red Bay series. It is probably most nearly related to *C. corystis,* the oldest known *Cephalaspis* species in Spitsbergen, and the similarities are fairly obvious, *C. isachseni* differs mainly by the smaller size, the narrower shield, the longer cornua and by the shorter inter-zonal part.

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, C. Kjeldsen division (lower part).

Locality. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier.

The single specimen was collected during the ENS expedition in 1939.

39. *Cephalaspis curta* n. sp.

(Fig. 60; pl. 47:2-3.)

Diagnosis. — A *Cephalaspis* species of small size with maximum breadth of cephalic shield somewhat less than twice as great as length of shield in median line. Shield rather rapidly narrowing

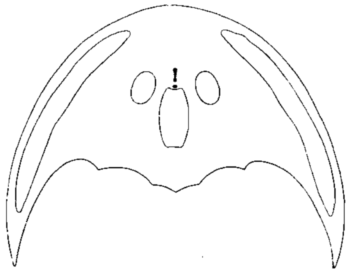


Fig. 60. — *Cephalaspis curta* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (ENS no. 569). Nat. size.

anteriorly, rostral margin rather obtusely rounded, without rostral angle; lateral margins convex. Cornua projecting in posterior and slightly lateral direction, their length contained about two and a half times in distance of their tips from rostral end of shield. Inner margins of cornua without denticles. Pectoral sinus broad and very shallow. Inter-zonal part broad and very short, dorsally with short, low median ridge; posterior angle protracted somewhat behind postero-lateral angles. Dorsal sensory field rather broad, not fully twice as long as broad. Lateral sensory fields extending backwards to middle of length of cornua. Orbital openings large, situated somewhat before middle of length of shield in median line. No pineal plate. Exoskeleton without ornamentation; superficial layer continuous. Mucous canal system enclosed in exoskeleton, consisting of fine-meshed network.

Holotype. — Cephalic shield (ENS no. 569).

Material. — The material of this species comprises two specimens (ENS nos. 568—569). The holotype (no. 569, pl. 47:2-3) consists of a rather complete cephalic shield in counterpart, lacking a small antero-lateral portion. No. 568 consists of an imperfect shield in counterpart, wanting a posterior portion and the left cornu, and is furthermore crushed and distorted. Two specimens (ENS nos. 570—571), consisting of cephalic fragments are placed here with much doubt.

The holotype has the following dimensions. The length of the shield in the median line is about 25 mm; the maximum breadth of the shield, lying between the middle parts of the cornua, is about 45 mm; the breadth of the inter-zonal part between its postero-lateral angles is 19.3 mm; the height of the shield at the posterior angle of the inter-zonal part is 11.5 mm; the distance of the pineal foramen from the posterior end of the shield is 14 mm. No. 568 is slightly smaller than the holotype. It is thus evident that the species attained only a small size.

Taken as a whole the shield is broad and short; its maximum breadth is not quite twice as great as the length of the shield in the median line. The shield decreases fairly rapidly in breadth towards the rostral margin, but this margin is fairly broad and is rather obtusely curved; there is no rostral angle. The lateral margins are distinctly convex. The cornua, which issue in a posterior and only slightly lateral direction, are rather short and stout, their length constitutes about $\frac{2}{5}$ of the distance of their tips from the rostral end of the shield; they reach far behind the posterior end of the inter-zonal part. The cornua are only slightly curved, the outer margins are rather convex but the inner margins fairly straight. The inner borders of the cornua are devoid of denticles. The pectoral sinus are broad and very shallow, with an indistinct, rounded antero-median corner. The inter-zonal part is very short, broad and fairly high; its breadth between the postero-lateral angles is nearly half as great as the maximum breadth of the shield. The posterior angle of the inter-zonal part is very obtuse, the posterior end reaches backwards only somewhat behind the postero-lateral angles. Dorsally the inter-zonal part is provided with a very low median ridge, which begins somewhat behind the dorsal sensory field, reaches backwards, and constitutes the extreme posterior end of the inter-zonal part. The dorsal sensory field is comparatively short and broad; its breadth constitutes somewhat more than half of the length of the field; it is broadest in its middle part, has convex lateral margins, and truncated anterior and posterior ends. The length of the field is somewhat greater than the distance of its posterior margin from the posterior end of the shield. The lateral sensory fields are of fairly uniform breadth and rather long, reaching backwards to the middle of the length of the cornua. The orbital openings are large, roundedly oval in shape, and placed somewhat in front of the middle of the length of the shield in the median line; the distance of an orbital opening from the rostral end of the shield being about equal to that from the pectoral sinus. The inter-orbital breadth is about one and a half times as great as the transverse diameter of an orbital opening. There is no independent pineal plate. The circum-nasal fossa is triangular, and fairly deep anteriorly.

All over the shield the exoskeleton seems to be without any ornamentation. The superficial layer forms a continuous covering to the middle layer. The radiating canals are disposed in distinct bundles and form vascular areas of somewhat varying size; they seem on the average to measure 0.9 mm in diameter. No ringsinus are observed in the basal layer. The mucous canal system is enclosed in the exoskeleton and forms a network of very fine, uniform canals.

The endoskeleton is very imperfectly preserved or was only slightly ossified. Only some traces of the superficial canals are to be seen; the canal vls_3 enters the orbit at its very postero-dorso-lateral corner, and the canals vls_4 and vls_5 join in median direction into a common trunk.

Remarks. — *C. curta* is not a very characteristic species. It differs from its congeners by a combination of characters, pointed out in the diagnosis. Among the Cephalaspids from the Wood Bay series it is, however, distinguished by its small size. In the general shape of its shield the species takes a position about midway between *C. platyce-*

phalus on one side, and *C. menoides* and *C. semicircularis* on the other; besides the fact that it is much smaller, it differs from all of them by the short and broad inter-zonal part, and by the shape of the dorsal sensory field; it seems, however, to be most closely related to *C. platycephalus*.

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, lower part of the C. Kjeldsen division.

Localities. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier, in a grey sandstone near the shore (in one piece of rock, nos. 568—569), in a red sandstone (no. 570, doubtfully placed here). E. side of Wood Bay: Stjørdalen Valley, S. side (no. 571, doubtfully placed in this species).

All the specimens were collected by the ENS expedition in 1939.

40. *Cephalaspis fracticornis* n. sp.

(Fig. 61; pls. 44:1; 47:1.)

Diagnosis. — A *Cephalaspis* species of large size with maximum breadth of cephalic shield about twice as great as length of shield in median line. Shield very rapidly narrowing forwards. Rostral margin broad, slightly convex, without rostral angle. Obtusely rounded angle present on lateral margins at transition between main shield and cornua. Cornua stout and flat, projecting in posterior direction, reaching backwards behind posterior end of shield. Length of cornua probably constituting about one-third of distance of their tips from rostral end of shield. Pectoral sinus broad and shallow. Inter-zonal part very narrow and short, its breadth being contained slightly more than three times in maximum breadth of shield. Dorsal sensory field small, lateral fields very broad posteriorly, with rounded postero-median angle on zonal part in front of pectoral sinus. Orbital openings comparatively small, situated at about middle of length of shield in median line. No pineal plate. Exoskeleton with smooth, continuous superficial layer. Mucous canal system enclosed in exoskeleton.

Holotype. — Cephalic shield (ENS no. 572).

Material. — Besides the holotype (ENS no. 572), the species is represented by only one specimen (ENS no. 573). The holotype (pl. 44:1) consists of a fragmentary shield, lacking most of the rostral and the right parts, and also the end of the left cornu. No. 573 (pl. 47:1) is very imperfect and much distorted by pressure in the rock, only parts of the cornua and the very lateral and rostral borders of the shield being preserved.

Description. — Very few exact measurements can be taken on the holotype. The length of the shield in the median line can be estimated at about 75 or 80 mm; the maximum breadth of the shield was about 160 mm. The breadth of the inter-zonal part was about 50 mm and its height at the posterior end at least 23 mm. The distance of the pineal foramen from the posterior end of the shield is 38 mm. The other shield is too imperfect as to allow of any measurements to be taken but is evidently of about the same size as the holotype shield. The species has thus attained a large size.

Taken as a whole the cephalic shield is very broad in proportion to its length, with a maximum breadth which is about twice as great as the length of the shield in the median line. The shield decreases rapidly in breadth forwards from the bases of the cornua. The rostral margin is not preserved in the holotype but was obviously very broad, and from the preserved parts as well as from its configuration in no. 573 it can be stated that the rostral margin in the species is obtusely rounded without any rostral angle. There were no angles or very obtuse and rounded ones at the transition from the rostral to the lateral margins. The lateral margins are very slightly convex. At the transition of the lateral margins of the main shield into those of the cornua is formed an obtuse and rounded angle since the cornua are directed in a much more posterior direction than the lateral margins of the main shield. The cornua thus project in a straight posterior or in a posterior and only slightly lateral direction, and reach backwards rather far behind the posterior end of the inter-zonal part; the distal ends of the cornua are wanting but it is evident that the cornua were fairly long with a length that is probably contained about three times in the distance of their tips from the rostral end of the shield. The cornua are very broad in their proximal parts and flattened dorso-ventrally, their inner and outer margins were very probably converging in straight lines towards the tip; in no. 573 the dorso-medial borders of the cornua are provided with few and very small denticle-like tubercles, much like those in *C. laticornis*. The pectoral sinus are very broad and shallow, in the holotype with a very obtuse and indistinct antero-lateral corner. The inter-zonal part is very short and rapidly decrases in breadth backwards; its breadth between the postero-lateral angles constitutes somewhat less than one-third of the maximum breadth of the shield. The height of shield at the posterior end of the inter-zonal part is comparatively great, or about half as great as the breadth of the inter-zonal part. Dorsally the inter-zonal part was very probably provided with a low, broad, and indistinctly defined median ridge. The sensory fields are well developed but on account of the imperfect preservation of the shield rather little can be said about their shape. It is obvious that the dorsal field must have been very small in proportion to the size of the shield, and its probable shape is restored in fig. 61. The lateral sensory fields reach backwards over tre proximal part of the cornua; their shape in the anterior parts cannot be determined, but posteriorly, in front of the pectoral sinus they

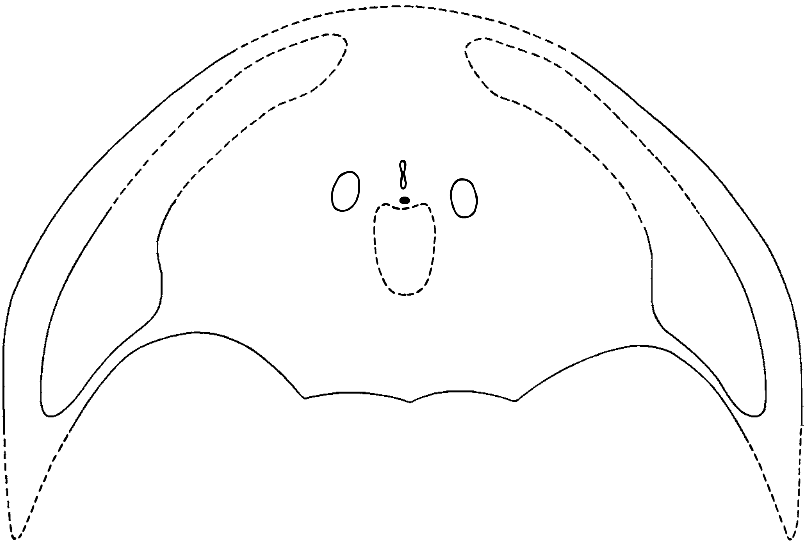


Fig. 61. — *Cephalaspis fracticornis* n. sp. Restoration of the cephalic shield in dorsal view. After the holotype (ENS no. 572). ⅔.

widen rather strongly; thus a well marked bulge is formed on the median side of the fields, which in this respect remind of those of *C. metopias.* The orbital openings are comparatively small, and situated about midway between the rostral and the posterior end of the shield. There is no independent pineal plate developed. The inter-orbital region is much crushed and imperfectly preserved to that nothing can be said about the shape of the naso-hypophyseal opening; the circum-nasal fossa seems, however, to be very broad and shallow.

The development of the exoskeleton could not be studied in the holotype on account of the imperfect preservation of its shield. In the second specimen (no. 573) some details of the minute structure of the exoskeleton are revealed in some small spots on the periphery of the shield, and it is impossible to say if the same conditions were prevalent also on the major parts of the shield. In front of the pectoral sinus the superficial layer is preserved; it forms a continuous covering to the middle layer and the outer face is quite smooth. Along the margins of the shield, the middle layer is provided with vascular canals running parallelly to the margin; in one place some of these canals are seen to open into obliquely running larger canals, probably issuing from the subcutaneous canal plexus (pl. 47:1). The mucous canal system is enclosed in the exoskeleton at least in front of the pectoral sinus; at the lateral margin, however, are observed open grooves or only partly closed canals, belonging to the mucous canal system; otherwise nothing can be said of its development.

Almost nothing is preserved of the endoskeleton, and it seems to have been only poorly ossified.

Remarks. — Characterized by the broad cephalic shield, in connection with the narrow and comparatively high inter-zonal part, and the posteriorly directed (as if fractured) stout cornua and the shape of the lateral sensory fields, *C. fracticornis* cannot be confused with any of the known *Cephalaspis* species. The general shape of the shield may recall that of *C. lata,* as restored by Stensiö (1927, fig. 60), but, even if this species is very imperfectly known, it is, nevertheless, evident that the two species are quite distinct. It is quite unsettled where the nearest relatives to *C. fracticornis* are to be found.

Geological horizon. — Upper Eodevonian: Wood Bay series, the C. Kjeldsen division.

Localities. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier (no. 572); Mt Kronprinz, opposite Stjørdalen Valley (no. 573).

Both specimens were collected by the ENS expedition in 1939.

41. *Cephalaspis brevicornis* Stensiö ?

(Fig. 62; pl. 46:1.)

1927. *Cephalaspis brevicornis,* Stensiö, p. 257; fig. 59; pls. 4:2; 5:1-2; 12.

Holotype. — Cephalic shield (no. 8) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 257).

Material. — Under this name I place hesitatingly one specimen (ENS no. 574). It consists of the dorsal exoskeleton of the left half of a cephalic shield, the anterior and posterior margins are imperfect and the distal part of the cornu is lacking; the exoskeleton, which is exposed in ventral view, is much worn and abraded.

Remarks. — The original description of this species was based on four very fragmentary cephalic shields (nos. 7, 8, 13, 56 in the Palaeontological Museum, Oslo). Our knowledge of the species is as yet very limited and it is impossible to give an adequate specific diagnosis. It appears to me not at all certain that the four fragments belong to one and the same species; I am thus fairly positive that no. 13 represents a different species. The holotype is in fact so poorly preserved that it will be very difficult to compare new and better preserved shields with it and thereby assign them with any certainty to this species. *C. brevicornis* will probably in all future remain a problematic species. — In the new material at hand, there is one fragmentary shield (no. 574), which can to some extent be compared with *C. brevicornis,* viz. with no. 7 placed by Stensiö in this species (Stensiö 1927, pl. 4:2). An attempted restoration based on this shield is given in fig. 62; restored

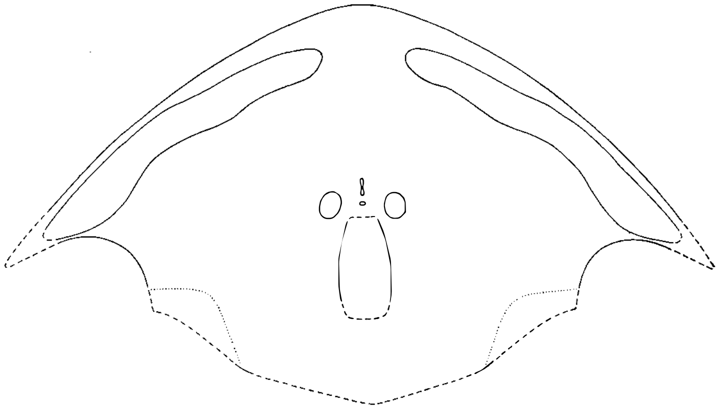


Fig. 62. — *Cephalaspis brevicornis* Stensiö ? Attempted restoration of the cephalic shield, dorsal view. The dotted lines mark the postero-lateral borders of the endoskeleton. After ENS no. 574. ⅓.

in this way, it agrees fairly well with the restoration given by Stensiö (1927, fig. 59). The shield is somewhat smaller than the holotype but seems to be of the same size as Stensiö's specimen no. 7; it is very broad, probably about twice as broad as long; the inter-zonal part too is broad, half or somewhat more than half as broad as the maximum breadth of the shield. The dorsal sensory field is apparently rather broad and short. The lateral sensory field lies in its anterior half somewhat more distant from the lateral margin of the shield than does its posterior part; posteriorly the field is somewhat widened before it tapers rather rapidly towards the end, which lay just behind the preserved posterior end of the cornua; thus the field probably reached to the middle of the length of the cornua. The orbital openings are rounded in shape and probably situated about midway on the shield. The distance of the left orbital opening from the pectoral sinus is 7.2 cm. There is no independent pineal plate. The ornamentation of the exoskeleton is observed only at a few places along the lateral margin where it consists of flattened tubercles, suggestive of those in Stensiö's specimen no. 13 (Stensiö 1927, pl. 12). As is seen from these short notes there are many obscure points in our knowledge which must be made clear before we can get an approximate conception of this form, no matter whether it belongs to the species *C. brevicornis* or not.

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, the lower part of the C. Kjeldsen divsion.

Locality. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, E. slope, 0—500 m.

The single specimen was collected by the ENS expedition in 1939.

42. *Cephalaspis producta* n. sp.

(Fig. 63; pl. 43:1.)

Diagnosis. — A *Cephalaspis* species of moderately large size, with maximum breadth of cephalic shield somewhat greater than length of shield in median line. Shield narrow, decreasing in breadth forwards; rostral margin narrow; rostral angle present. Lateral margins slightly convex. Cornua projecting in posterior and slightly lateral direction, moderately long, their length being contained somewhat less than three times in distance of their tips from rostral angle. Inner margins of cornua without denticles. Pectoral sinus very shallow, with antero-median corner. Inter-zonal part very short, rather narrow, its breadth being contained about two and one-third times in maximum breadth of shield; postero-dorsal portion with small posteriorly inclined median spine. Dorsal sensory field elongate, two and a half times as long as broad. Lateral fields tapering towards pointed posterior end. Orbital openings of moderate size, situated distinctly in front of middle of length of shield in median line. No independent pineal plate present. Mucous canal system in main parts of shield differentiated into circum-areal and intra-areal canals. Polygonal areas very small, of varying shape.

Holotype. — Cephalic shield (ENS no. 575).

Material. — The available material of this species consists of one specimen, the holotype (ENS no. 575, pl. 43:1), being represented by an almost complete but poorly preserved and somewhat distorted cephalic shield in counterpart. A second specimen (ENS no. 576), consisting of a fragmentary and crushed shield, is placed here with some doubt.

Description. — The holotype is somewhat distorted by pressure in the rock. The measurements given below refer to the shield in its present state. The length of the shield from the rostral end to the posterior margin of the preserved portion of the dorsal spine on the inter-zonal part is 93 mm, the maximum breadth, which lies between the middle parts of the cornua, is 115 mm. The distance of the tip of each cornu from the rostral end of the shield is 135 mm and about 123 mm, respectively. The breadth of the inter-zonal part between the postero-lateral angles is 50 mm. The height at the posterior end of the inter-zonal part is about 25 mm (the dorsal spine not included).

In general shape the cephalic shield is rather narrow in proportion to its length, the maximum breadth being only somewhat greater than the median length of the shield, or, more precisely, slightly less than one and a quarter times of this length. The shield narrows moderately towards the rostral margin, which is narrow and very convex. In its present state, the shield exhibits a distinct rostral angle and also an obtuse and indistinct angle at the transition from the rostral to the left

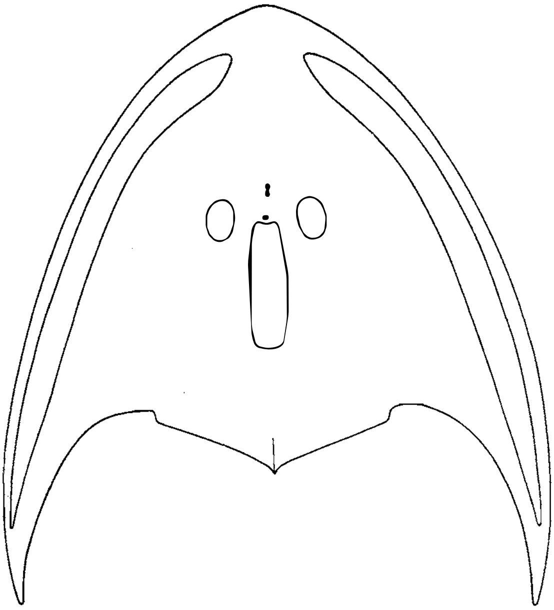


Fig. 63. — *Cephalaspis producta* n. sp. Restoration of the cephalic shield, dorsal view. Mainly after the holotype (ENS no. 575). ⅔.

lateral margin; it is, however, probable, that in the original condition of the shield at least the latter angle was absent. The lateral margins of the shield are slightly curved. The cornua, which are of a moderate length, project in posterior and very slightly lateral direction, and reach far behind the posterior end of the inter-zonal part; their length constitutes somewhat more than one-third of the distance of their tips from the rostral end of the shield. They are flattened dorso-ventrally, and taper fairly rapidly and uniformly towards their slender distal parts which are slightly curved in median direction; their inner margins are devoid of denticles. The pectoral sinus are rather broad but very shallow, they are provided with a distinct antero-median corner, and the shape of the sinus is thus much as in *C. hoeli.* The inter-zonal part is very short and comparatively narrow; its breadth is somewhat more than half the maximum breadth of the shield. The posterior angle of the inter-zonal part extends backwards to a distance only slightly behind the postero-lateral angles. In the most posterior portion, the inter-zonal part is provided with a small dorsal spine. Only the most basal part of the spine is preserved but, to judge from that part, it must have been rather small and backwardly inclined. The dorsal sensory field is badly exposed in the holotype and its exact shape is here not very clear but in the second specimen (no. 576) the field is elongate in shape, rather narrow and about two and a half times as long as broad; the lateral margins are almost straight, the posterior margin is roundly truncated, and the anterior margin is emarginate behind the pineal foramen. The distance of the posterior margin of the field from the posterior end of the shield is about equal to the length of the field. The lateral sensory fields are of moderate breadth anteriorly; from there they taper gently backwards, being thus very narrow and pointed posteriorly; they end on the distal part of the cornua at some distance before the tips of the cornua. The distance between the antero-median ends of the two lateral fields is very short, being about as great as the inter-orbital breadth. The orbital openings are of a medium size, elongately oval in shape, and situated nearer to the rostral end of the shield than to the posterior end of the inter-zonal part. There is no independent pineal plate. The pineal foramen lies rather far behind the naso-hypophyseal opening before the sinus of the anterior margin of the dorsal sensory field. The circum-nasal fossa is shallow and indistinctly bordered.

The exoskeleton is very impertfectly preserved. It could not be established whether the superficial layer is continuous or not in the greater and central portions of the shield. On some places along the very margins of the rostral and lateral parts it seems as if the superficial layer were forming a continuous covering to the middle layer. The middle layer has well developed radiating canals. It could not be ascertained if the mucous canal system is entirely enclosed in the exoskeleton or not; in the greater portion of the shield it is differentiated into circum-areal and intra-areal canals or grooves. The circum-areal canals (or grooves) encircle very small polygonal areas, with an average diameter of 0.7 mm; in the space between the lateral sensory fields and the lateral margins of the shield the polygonal areas are much lengthened, being two or three times as long as broad. In no. 576, close to the inner margin of the orbit, the mucous canals (or grooves) form a uniform rather wide-meshed network.

The endoskeleton is in a very imperfect state of preservation, parts of the post-branchial wall are, however, seen in the holotype.

Remarks. — *C. producta* resembles the British species *C. lankesteri* (Stensiö 1932, p. 123) and *C. websteri* (Stensiö 1932, p. 133), and to some extent *C. agassizi* (Stensiö, p. 125). It differs from *C. lankesteri* mainly by the larger size of its shield and by the shape of the pectoral sinus and the inter-zonal part, as well as by the development of the mucous canal system, from *C. websteri* i. a. by the shape of the cornua, the dorsal spine, and the lateral sensory fields; it can also be noted that both these species have an independent pineal plate, contrary to what is the case in *C. producta*. From *C. agassizi* it differs i. a. by the shape of the inter-zonal part, the cornua, and the lateral sensory fields. Among the Spitsbergian Cephalaspids it reminds slightly of *C. acuminata* (p. 258), *C. eukeraspidoides* (p. 302), and *C. oblonga* (p. 393) and is probably closely related to this latter species, but differs from it by the longer and narrower cephalic shield, the shape of the inter-zonal part and of the cornua.

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, lower part of the C. Kjeldsen division.

Localities. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier (no. 575). E. side of Wood Bay: Mt Scott Keltie, N. part, W. slope (no. 576, hesitatingly placed in this species).

The two specimens were collected by the ENS expedition in 1939.

43. *Cephalaspis oblonga* Stensiö.

(Fig. 64; pl. 48:2-3.)

1927. *Cephalaspis oblongus,* Stensiö, p. 250; fig. 55; pl. 2:2.

Diagnosis. — A moderately large *Cephalaspis* species with maximum breadth of cephalic shield nearly one and a half times as great as length of shield in median line. Shield fairly rapidly narrowing forwards. Rostral margin narrow, well rounded without rostral angle. Lateral margins curved. Cornua broad and long, projecting in posterior and somewhat lateral direction, reaching far behind posterior angle of inter-zonal part; length of cornua constituting nearly half of distance of their tips from rostral end of shield. Inner margin of cornua without denticles. Pectoral sinus narrow. Inter-zonal part narrow, its breadth contained somewhat more than three times in maximum breadth of shield; posterior angle reaching backwards far behind postero-lateral angles. Dorsal sensory field elongate with parallel lateral sides. Lateral sensory fields narrow, tapering towards pointed ends on distal parts of cornua. Orbital openings situated before middle of length of shield in median line. No pineal plate. Outer parts of exoskeleton absent. Mucous canal system not enclosed in exoskeleton.

Holotype. — Imperfect cephalic shield (no. 3) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 250).

Material. — To this species I refer one specimen (ENS no. 577, pl. 48:2). It consists of an imperfect cephalic shield, lacking most of its left side and the tip of the right cornu; it is preserved in ventral view. Besides this specimen I place here with some hesitation four specimens, ENS nos. 578, 579 (pl. 48:3), 580—581, consisting of very imperfectly preserved cephalic shields, one (no. 579) being also distorted by pressure of the rock. — I have also had the opportunity to restudy the holotype shield, which seems to be slightly distorted.

Description. — No exact measurements can be taken of the new specimen. As here restored (fig. 64) the length of the shield is estimated at about 80 mm and the maximum breadth at about 115 mm. The inter-zonal part is about 35 mm broad. The shield is only slightly smaller than the holotype shield. On the whole the shields belonged to a fairly large species.

The cephalic shield is rather broad with a maximum breadth (which lies between the distal parts of the cornua) that is about one and a half times as great as the length of the shield in the median line; on the whole the shield has the form of an almost equilateral triangle, the distance of the tip of the cornua from the rostral end of the shield is very slightly greater than the maximum breadth of the shield. The shield narrows rather rapidly forward with fairly curved lateral margins. The rostral margin is rather narrow and convex but without any rostral angle. The cornua, which are broad and long, project in a posterior and somewhat lateral direction and reach far behind the posterior end of the inter-zonal part; they are much flattened dorso-ventrally and on their median margins provided with a fairly broad cornual shelf without denticles. The length of the cornua is contained somewhat more than twice in the distance of their tips from the rostral end of the shield. The pectoral sinus are rather narrow and fairly deep; they are somewhat asymmetrically developed but there is no distinct antero-median corner. The inter-zonal part is rather short and strikingly narrow; its breadth between the postero-lateral angles constitutes very slightly less than one-third of the maximum breadth of the shield. The postero-dorso-median portion of the inter-zonal part is protracted backwards as a median process, and the posterior angle lies thus far behind the postero-lateral angles. Dorsally the inter-zonal part is provided with a long, very low median ridge but, as the most posterior portion of the inter-zonal part is missing, it cannot be ascertained whether this ridge continued backwards as a spine or not. The dorsal sensory field is elongate in shape and about two and a half times as long as broad; the lateral margins are almost parallel, and the posterior margin very probable was convex. The distance of the posterior margin of the field from the posterior end of the shield cannot be measured but was evidently greater than the length of the field. The lateral sensory fields are narrow with their greatest breadth in the anterior part; they decrease very gradually in breadth backwards and terminate with narrowly pointed ends on the distal parts of the cornua somewhat before their tips. The orbital openings, which are oval in shape, lie distinctly before the middle of the length of the shield but their distance from the rostral end of the shield is slightly greater than that from the pectoral sinus. The inter-orbital breadth is about twice as great as the transverse diameter of an orbital opening. No independent pineal plate was developed. The circum-nasal fossa is fairly well defined in the holotype.

The exoskeleton is in a very bad state of preservation. It seems, however, probable that both the superficial layer and the outer division of the middle layer were absent. The lower division of the middle layer

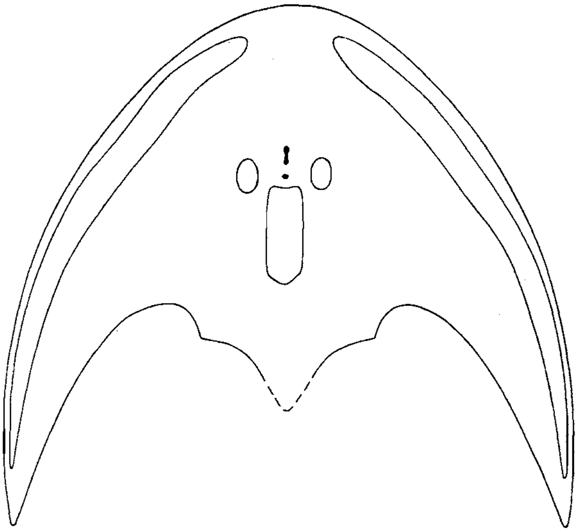


Fig. 64. — *Cephalaspis oblonga* Stensiö. Restoration of the cephalic shield, dorsal view. After ENS no. 577 and the holotype (Pal. Mus. Oslo no. 3). ⅔.

contains radiating vascular canals of an extremely fine calibre; as observed on the basis of the cornu, they are disposed in fascicles and form distinct vascular areas; the distance between the centres of two such areas was measured and found to be 2.3 mm. The mucous canal system lay very propably entirely outside the exoskeleton and nothing can be said about its development.

Of the endoskeleton only some traces of the linings of the superficial canals are observed in no. 579, doubtfully placed in this species. The canal sel_1 is as usual divided into two branches just antero-laterally to the orbit; the nerve canals of the lateral sensory fields are on the whole disposed in three groups, each consisting of two canals running close together; the first group comprises the two branches of the canal sel_1, the second group the canals sel_2 and sel_3, and the third group the canals sel_4 and sel_5.

Remarks. — From the new and more complete material, now at hand, it is seen that the cephalic shield of *C. oblonga* has a shape somewhat different from that given in the restoration by Stensiö (1927, fig. 55); a new restoration of the shield is given in fig. 64; it can be noted that this restoration, which is mainly based on the new specimen no. 577, is also in agreement with the conditions in the holotype.

It is now seen that the shield of *C. oblonga* resembles in many points that of *C. producta* (p. 390) and *C. moy-thomasi* (p. 396); and it seems probable that *C. oblonga* is in some way closely related to these species, and also, somewhat more distantly, to *C. borealis, C. semicircularis, C. høegi,* and their allies. *C. oblonga* differs from *C. producta* by its broader shield, more stoutly built cornua, the shape of the pectoral sinus and the inter-zonal part, and from *C. moy-thomasi* by its longer and narrower shield, the narrower pectoral sinus and the inter-zonal part. Fragments of the shields of *C. oblonga* and *C. moy-thomasi* can be very difficult to distinguish, especially if they are somewhat distorted. Here can also be emphasized that similarities exist between *C. pinnifera* (p. 370) and *C. oblonga* together with other *Cephalaspis* species from the Wood Bay series, mainly in the shape of the lateral sensory fields.

Geological horizon. — Upper Eodevonian: Wood Bay series, the C. Kjeldsen division.

Localities. — Spitsbergen. E. side of Bock Bay: Mt Kronprinz, W. slope (no. 577). — The localities for the specimens, doubtfully placed in this species, are: W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier (no. 580), E. slope, 0—500 m (nos. 578, 581). E. side of Wood Bay: Mt Wächter, slope towards Wood Bay (no. 579).

All the specimens were collected by the ENS expedition in 1939.

44. *Cephalaspis moy-thomasi* n. sp.

(Fig. 65; pl. 49:2.)

Diagnosis. — A *Cephalaspis* species of moderately large size with maximum breadth of cephalic shield about one and a half times as great as length of shield in median line. Rostral margin fairly broad and convex without rostral angle. Lateral margins rather strongly curved. Cornua long and fairly stout, projecting in posterior direction, reaching far behind posterior end of inter-zonal part; their length somewhat less than half of distance of their tips from rostral end of shield. Inner margin of cornua without denticles. Pectoral sinus broad and fairly shallow. Inter-zonal part narrow, its posterior breadth contained nearly three times in maximum breadth of shield. Posterior angle of inter-zonal part protracted slightly behind postero-lateral angles. Dorsal sensory field elongate, about twice as long as broad, with parallel lateral margins. Lateral sensory fields rather narrow, extending backwards to posterior parts of cornua, tapering towards posterior pointed ends. Orbital openings situated in front of middle of length of shield in median line. No pineal plate present. Mucous canal system situated in circumareal grooves and in intra-areal canals (or grooves).

Holotype. — Distorted cephalic shield (ENS no. 582).

Material. — The available material of this species consists of two specimens (ENS nos. 582—583). The holotype (no. 582, pl. 49:2) is represented mainly by the complete dorsal exoskeleton (exposed in ventral view) of a shield, which is rather much distorted by pressure in

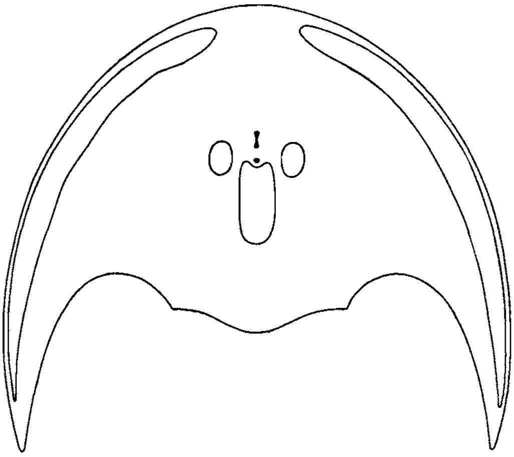


Fig. 65. — *Cephalaspis moythomasi* n. sp. Attempted restoration of the cephalic shield, dorsal view. After the holotype (ENS no. 582). ⅔.

the rock. The second specimen (no. 583) consists of the dorsal exoskeleton of a fragmentary shield also much distorted by pressure.

Description. — As the cephalic shields are much affected by pressure in the rock the obtainable measurements must be used with caution. They are, however, given here. The length in the median line is 67 mm (no. 582) and 73 mm (no. 583); the maximum breadth is 113 mm (no. 582), the breadth of the inter-zonal part is 38 mm (no. 582), and the distance of the pineal foramen from the rostral end of the shield is 30 mm (no. 582) and 35 mm (no. 583). The shields have thus belonged to a species of a moderately large size.

In general appearance the shield is rather broad and low, and the maximum breadth (which lies between the middle parts of the cornua) is about one and a half times as great as the length of the shield in the median line and about equal to the distance of the rostral end from the tips of the cornua. The shield decreases fairly rapidly in breadth forwards with rather strongly curved lateral margins. The rostral margin is rather broad and obtusely rounded without any rostral angle. There are no angles at the transition between the rostral and the lateral margins. The cornua, which are long and fairly stout, and dorso-ventrally flattened, project in a posterior direction and reach backwards far behind the posterior end of the inter-zonal part. The length of the cornua is contained somewhat more than twice in the distance of their tips from the rostral end of the shield. The cornua are rather broad basally and taper gently and uniformly towards their tips, the distal parts being very slightly curved in median direction; their inner margins are devoid of denticles. The pectoral sinus are comparatively broad and rather shallow; they are uniformly concave. The inter-zonal part is short; it narrows rapidly backwards and the posterior breadth constitutes slightly more than one-third of the maximum breadth of the shield. The inter-zonal part is protracted slightly backwards and reaches only inconsiderably behind the postero-lateral angles; the posterior angle is broadly rounded. In the holotype there is no trace of a dorsal median ridge; in no. 583, however, there is a fairly distinct indication of a ridge starting from a point somewhat behind the posterior border of the dorsal sensory field and running backwards for some distance. The dorsal sensory field is elongate in shape, with parallel lateral margins, concave anterior and rounded posterior margin; it is slightly more than twice as long as broad. The anterior margin lies closely behind the pineal opening and the distance of the posterior margin from the posterior end of the shield is about equal to the length of the field. The lateral sensory fields are rather narrow; they are situated near to the lateral margins of the shield and reach backwards to the distal parts of the cornua; posteriorly they taper gently towards their narrowly pointed ends. The distance between the antero-median ends of the two fields is about one and a half times as great as the inter-orbital breadth. The orbital openings, which are of a moderate size and oval in shape, are situated nearer to the rostral than to the posterior end of the shield and somewhat nearer to the pectoral sinus than to the rostral end. There is no independent pineal plate present, and the pineal foramen lies in the distinct sinus of the anterior margin of the dorsal sensory field. The circum-nasal fossa is narrowly triangular in shape, rather deep anteriorly, and shallow and ill-defined posteriorly.

The exoskeleton is imperfectly preserved in both specimens, and thus very little can be said about its structure. In the holotype the outer face of the exoskeleton seems to be without any coarse tuberculation, and is quite smooth at least along the lateral margins. In no. 583, however, the ornamentation consists of tubercles, one rather large tubercle in each polygonal area; in the posterior parts of the shield there are also small tubercles between the large ones and in the posterior portion of the inter-zonal part the tuberculation is rather irregular. On the cornua the ornamentation consists of scattered comparatively large tubercles and many small tubercles which here are all more or less elongated. In the holotype well developed radiating canals are observed in the middle layer. The basal layer contains no ringsinus. The mucous canal system is situated in open circum-areal grooves and in intra-areal canals (or grooves); it could not be ascertained whether the latter are wholly enclosed in the exoskeleton or not. The polygonal areas formed by the circum-areal grooves are comparatively small, the average diameter (in both the holotype and in no. 583) being 1.6 mm.

The endoskeleton is very imperfectly preserved in the holotype and nothing can be said of the inner anatomical details.

Remarks. — *C. moy-thomasi* is characterized by the rather broad cephalic shield, the direction and the shape of the long and stout cornua, and by the narrow inter-zonal part. It can be noted that no. 583, in which the ornamentation differs from that in the holotype, may represent a variety or subspecies of itself; the material is, however, too scanty as to allow a subdivision of the species; it may be sufficient here only to note the difference.

The species closely resembles *C. oblonga* (p. 393), *C. semicircularis* and *C. menoides* (p. 402), and from the systematic point of view seems to occupy an intermediate position between the two former species. It differs from *C. oblonga* by its broader and shorter shield, the slenderer cornua and by the shape of the inter-zonal part, and from *C. semicircularis* and *C. menoides* mainly by the longer shield and the shape of the cornua. It is of interest also to note that *C. moythomasi* in the general outline of its shield is extremely similar to *C. dawsoni* from the Upper Eodevonian (?) of Gaspé (Lankester 1870b) but as the latter species is very imperfectly known no closer comparison can be made; as seen from the figure by Lankester the shield of *C. dawsoni* is smaller and anteriorly more narrowing than in *C. moythomasi.*

C. moy-thomasi is named in memory of the late J. A. Moy-Thomas, who has contributed much to our knowledge of the Palaeozoic fishes; he was a member of the ENS expedition to Spitsbergen in 1939.

Geological horizon. — Upper Eodevonian?: Wood Bay series, the Stjørdalen division.

Localities. — Spitsbergen. E. side of Wood Bay: Mt Sørli (no. 582); Stjørdalen Valley, S. side, W. part (no. 583).

Both specimens were collected in 1939 by the ENS expedition.

45. *Cephalaspis semicircularis* n. sp.

(Fig. 66; pl. 48:1.)

Diagnosis. — A *Cephalaspis* species of moderate size with maximum breadth of cephalic shield twice as great as length of shield in median line. Shield rapidly narrowing forwards with rather strongly curved lateral margins. Rostral margin broad, obtusely rounded, without rostral angle. Cornua broad and flat, uniformly tapering towards their tips, projecting in posterior direction and reaching behind posterior end of inter-zonal part. Length of cornua constituting slightly less than half of distance of their tips from rostral end of shield. Inner margin of cornua without denticles. Pectoral sinus broad and shallow, with anteromedian corner. Inter-zonal part very short and narrow; its posterior breadth constituting about one-third of maximum breadth of shield; dorsally with low median ridge. Dorsal sensory field about twice as long as broad with almost parallel lateral margins and rounded posterior margin. Lateral sensory fields narrow, gently tapering towards narrowly pointed ends on distal parts of cornua. Orbital openings of moderate size, situated about halfway between rostral and posterior ends of shield. No pineal plate.

Holotype. — Cephalic shield (ENS no. 584).

Material. — The material, which I place in this species, consists of three specimens (ENS nos. 584—586). The holotype (no. 584, pl. 48:1) is represented by a cephalic shield in counterpart, lacking most of its left half; the other specimens consist of imperfect cephalic shields, distorted by pressure in the rock. One specimen (ENS no. 587), consisting of an imperfect and much distorted cephalic shield, is placed here with much doubt.

Description. — The length of the cephalic shield in the median line is about 40 mm in the holotype, sligthly less in no. 586, and in no. 585 the length is estimated at 55 mm. The maximum breadth is about 78 mm in the holotype, and the distance of the tip of the cornu from the rostral end of the shield in the same specimen is about 65 mm. The breadth of the inter-zonal part (between the postero-lateral angles) is 23 mm in the holotype. The height is very inconsiderable in all the specimens; it cannot be exactly measured, but in the holotype does not exceed 10 mm.

Taken as a whole the cephalic shield is very broad and flattened; the maximum breadth, which lies between the middle parts of the cornua, is about twice as great as the length of the shield in the median line and somewhat more than the distance of the tip of a cornu from the rostral end of the shield. The shield narrows rapidly forwards with the lateral margins rather strongly convex. The extreme rostral end is not preserved in the holotype, and is crushed and distorted in no. 585, but in no. 586 it is obtusely rounded without any rostral angle, and to judge from the shape of the preserved parts the same condition existed also in the holotype. The rostral margin is broad and passes without interruption gradually into the lateral margins. The cornua project in posterior direction, and reach far behind the posterior end of the inter-zonal part; they are rather long, stout and much flattened dorso-ventrally, and decrease uniformly in breadth towards their tips. The distal parts of the lateral margins of the cornua are very slightly curved medially so that the maximum breadth of the shield does not lie between the tips of the cornua but somewhat anteriorly to them. The length of the cornua is contained slightly more than twice in the distance of their tips from the rostral end of the shield. The median margins of the cornua are devoid of denticles. The pectoral sinus are broad and shallow, and in the holotype show a fairly distinct antero-median corner. The inter-zonal part is very short and narrow; its breadth between the postero-lateral angles is contained about three times in the maximum breadth

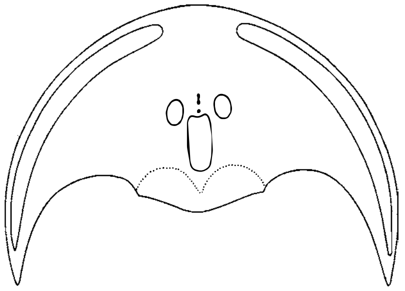


Fig. 66. — *Cephalaspis semicircularis* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (ENS no. 584). The dotted line indicates the posterior border of the endoskeleton. ⅔.

of the shield. On its dorsal side the inter-zonal part is provided with a low but rather distinct median ridge, reaching from the posterior end forwards to the posterior margin of the dorsal sensory field. The distance between the dorsal field and the posterior end of the shield is distinctly less than the length of the dorsal field and thus comparatively shorter than in *C. menoides.* The dorsal sensory field is elongate, slightly more than twice as long as broad, and of almost uniform breadth; the posterior margin of the field is rounded, and the anterior abruptly truncated or with a small median notch in front of which the pineal foramen is situated. The lateral sensory fields are not well exposed in any of the specimens; they seem, however, to be rather narrow; posteriorly they reach far backwards and end on the distal parts of the cornua, their posterior ends tapering uniformly almost to a point. The orbital openings, which are of medium size, are oval in shape; in the holotype they are situated at about the middle of the length of the shield in the median line and nearer to the pectoral sinus than to either the rostral or the posterior end of the shield; in the two other specimens, however, they lie slightly nearer to the rostral than to the posterior end of the shield. The circum-orbital ridge is well developed. An independent pineal plate is not present. The circum-nasal fossa is rather narrow and comparatively well defined.

The exoskeleton is very imperfectly preserved. In no. 585 it is observed that the ornamentation between the postero-median margin of an orbital opening and the dorsal sensory field consists of very small tubercles; in no. 586 the outer face of the exoskeleton on the antero-lateral margin of the shield is quite smooth without any ornament. The radiating canals are very fine-calibrated. In the posterior portion of the inter-zonal part in the holotype the basal layer of the exoskeleton (which here is not underlain by the endoskeleton) encloses somewhat irregularly shaped canals; they correspond certainly to the regular ringsinus found in other Cephalaspids. As to the mucous canal system very little is revealed; there are, however, observed traces of circum-areal canals or grooves; the polygonal areas, encircled by them, are comparatively larger than the corresponding areas in *C. menoides,* the diameter being about 1.4 mm.

Of the endoskeleton practically nothing is preserved; the extent of the endoskeletal component of the shield is, however, indicated by impressions on the basal layer of the inter-zonal dorsal exoskeleton (see fig. 66 where the posterior border of the endoskeleton is indicated by dotted lines).

Remarks. — *C. semicircularis* is very similar to *C. menoides* and is probably closely related to this species. It differs, however, somewhat in size, in the general shape of the shield, by the position of the orbits and the dorsal sensory field, and particularly by the shape of the cornua, which in *C. semicircularis* are stouter than in *C. menoides* and uniformly tapering towards their tips; also the endoskeletal component of the inter-zonal part is extending farther backwards in the last mentioned species. *C. semicircularis* is probably also related to the similar *C. moy-thomasi* (p. 396) but differs from this species mainly by the shorter and broader shield.

Geological horizon. — Upper Eodevonian ?: Wood Bay series, the Stjørdalen division.

Localities. — Spitsbergen. E. side of Wood Bay: Stjørdalen Valley, S. side (nos. 585—586, and no. 587, doubtfully placed in this species), S. side, W. part (no. 584).

All the specimens were collected by the ENS expedition in 1939.

46. *Cephalaspis menoides* n. sp.

(Fig. 67; pl. 49:1.)

Diagnosis. — A moderately large *Cephalaspis* species with maximum breadth of cephalic shield about twice as great as length of shield in median line. Shield rapidly narrowing forwards with rather strongly curved lateral margins. Rostral margin very broad. Cornua broad proximally, rather rapidly tapering towards slender, slightly medially curved distal parts; projecting in posterior direction, reaching behind posterior end of inter-zonal part. Length of cornua contained about twice in distance of their tips from rostral end of shield. Inner margins of cornua without denticles. Pectoral sinus broad and shallow. Inter-zonal part rather narrow, its posterior breadth constituting about one-third of maximum breadth of shield. Dorsal sensory field twice as long as broad, with almost parallel lateral margins, posterior margin convex. Lateral sensory fields narrow, extending backwards to distal parts of cornua, narrowing towards pointed posterior end. Orbital openings rather large, situated far in front of middle of length of shield in median line. No pineal plate. Exoskeleton with continuous superficial layer, ornamented with minute tubercles of varying size. Mucous canal system enclosed in exoskeleton, differentiated into circum-areal and intra-areal canals. Polygonal areas rather small.

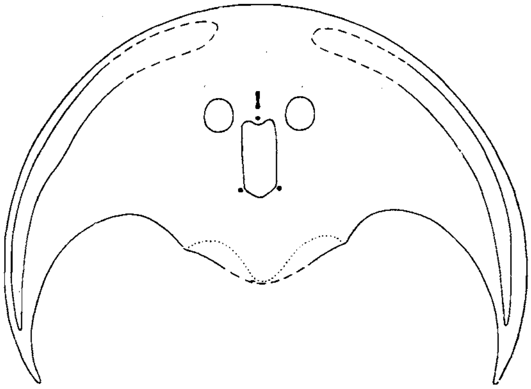


Fig. 67. — *Cephalaspis menoides* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (ENS no. 588). The dotted line indicates the posterior border of the endoskeletal component. ⅔.

Holotype. — Cephalic shield (ENS no. 588).

Material. — The species is represented by the holotype (ENS no. 588) only, which consists mainly of the dorsal exoskeleton of a rather complete cephalic shield, lacking the rostral part; it is exposed in ventral view.

Description. — The holotype has the following dimensions: The length of the shield in the median line cannot be directly measured but is estimated at about 55 mm; the maximum breadth of the shield is 105 mm and the posterior breadth of the inter-zonal part 33 mm. The distance of the tips of the cornua from the middle of the rostral margin is estimated at 98 mm. The height is apparently very insignificant.

In general appearance the cephalic shield is very broad and flat, and the maximum breadth, which lies between the middle parts of the cornua, is about twice as great as the length of the shield in the median line, and distinctly greater than the distance of the tip of a cornu from the rostral end of the shield. The shield rapidly decreases in breadth towards the rostral margin and the lateral margins are strongly convex. The most rostral parts of the shield are not preserved but it is evident that the rostral margin was very broad and probably was obtusely rounded without any rostral angle. The cornua, which project in posterior direction and reach much farther backwards than the posterior end of the inter-zonal part, are very broad and flattened dorso-ventrally in their proximal part. They taper rather rapidly towards their distal parts which constitute about a quarter of the length of the cornua; these parts are gently narrowing towards their tips and are distinctly curved in median direction. The inner margins of the cornua are devoid of denticles. The length of the cornua constitutes about half of the distance of their tips from the rostral end of the shield; they are thus rather long. The pectoral sinus are very broad and shallow, and uniformly concave without any corners. The inter-zonal part is narrow in proportion to the breadth of the shield and tapers rapidly towards its postero-lateral angles. The posterior breadth amounts to only about one-third of the maximum breadth of the shield. Dorsally the inter-zonal part is provided with a low, very indistinct median ridge, situated between a point some distance behind the posterior margin of the dorsal sensory field and the posterior end of the shield. The distance between the posterior margin of the dorsal field and the posterior end of the inter-zonal part is rather great, being about equal to the length of the field and thus comparatively greater than in *C. semicircularis.* The dorsal sensory field, which lies closely behind the pineal foramen, is about twice as long as broad and its lateral margins are almost parallel; the anterior margin is somewhat concave, and the posterior margin convex with an obtuse posterior angle. The openings for the ductus endolymphatici lie just outside the field near its postero-lateral corners. The lateral fields are narrow, and situated near to the lateral margins of the shield; they reach far backwards and taper gently towards their narrowly pointed distal ends on the distal half of the cornua but end somewhat more anteriorly than in *C. semicircularis.* The orbital openings, which are moderately large and roundedly oval in shape, are situated much nearer to the rostral than to the posterior end of the shield or to the pectoral sinus. The inter-orbital breadth is about one and a half times as great as the transverse diameter of an orbital opening. The circum-orbital ridge is rather well developed, but there is no antorbital prominence. No independent pineal plate is developed and the pineal foramen lies in the sinus of the anterior margin of the dorsal sensory field. The circum-nasal fossa is rather narrow and shallow.

The exoskeleton is rather badly preserved. The superficial layer is certainly continuous. The ornamentation of the outer face is at most very slightly developed and seems to consist of numerous minute tubercles. The radiating canals are very fine-calibrated. The mucous canal system is enclosed in the exoskeleton; it is differentiated into well defined circum-areal and a plexus of minute intra-areal canals. The polygonal areas defined by the circum-areal canals are very small, the average diameter of such an area being only 1.2 mm.

The endoskeleton is imperfectly preserved. The posterior border of the endoskeletal component of the shield in the inter-zonal part is indicated by an impression on the ventral face of the basal layer of the exoskeleton (it is indicated by a dotted line in the restoration, fig. 67); the endoskeleton extends farther backwards than in *C. semicircularis.*

Remarks. — *C. menoides* is characterized by the general shape of its broad crescentic cephalic shield and by the configuration of the cornua. It is very suggestive of *C. semicircularis* (p. 399) and resembles also *C. moy-thomasi* (p. 396) to some extent. From *C. semicircularis* it differs by the larger size of its shield, the more strongly rounded lateral margins, the shape of the cornua, the more anteriorly placed orbital openings and dorsal sensory field, and by the greater extent backwards of the endoskeleton in the inter-zonal part of the shield, and from the equally-sized *C. moy-thomasi* by the shape of the shorter and broader cephalic shield and the shape of the cornua, etc.

Geological horizon. — Upper Eodevonian (?): Wood Bay series, the Lyktan division.

Locality. — Spitsbergen. W. side of Dickson Bay: Mt Borgen, N. part.

The single specimen (no. 588) was collected by the ENS expedition in 1939.

47. *Cephalaspis laticornis* Stensiö.

(Fig. 68; pl. 50.)

1927. *Cephalaspis laticornis,* Stensiö, p. 255; fig. 58; pl. 4:1.

Diagnosis. — A *Cephalaspis* species of large size with very broad, flattened cephalic shield, the maximum breadth of which is somewhat more than twice as great as its length in median line. Shield rapidly narrowing anteriorly with curved lateral margins. Rostral margin very broad and obtuse, without any rostral angle. Cornua broad and flat, projecting in postero-lateral direction, reaching slightly behind posterior angle of inter-zonal part; their length being contained twice in distance of their tips from middle of rostral margin. Inner border of cornua in middle part with few, very short denticles. Pectoral sinus broad, rather deep. Inter-zonal part rather long, narrow; its breadth contained somewhat more than three times in maximum breadth of shield. Dorsal sensory field about twice as long as broad, abruptly narrowing in anterior half. Lateral sensory fields narrow, gently tapering towards pointed ends on distal parts of cornua. Orbital openings rather small, situated somewhat in front of middle of length of shield in median line. Outer face of exoskeleton without ornamentation.

Holotype. — Fragmentary cephalic shield (no. 6) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 255).

Material. — In the new material at my disposal *C. laticornis* is represented by three specimens (ENS nos. 589—591). They all consist of fragmentary shields; no. 589 (pl. 50:2) lacks the anterior and major part of the right side and is slightly distorted by pressure in the rock; no. 590 (pl. 50:1) lacks the anterior and most of the left side while no. 591 consists of an imperfect cornu with adjacent parts.

Description. — Although the cephalic shields are very incomplete, their study contributes nevertheless somewhat to the knowledge of the species.

On account of the imperfect state of preservation of the shields very few exact measurements can be taken. The length of the shield in the median line is estimated at about 70 mm and the maximum breadth at about 150 mm in no. 589. In the same specimen the breadth of the inter-zonal part is 40 mm, and the height of the shield is very small, not exceeding 15 mm. In no. 590 the breadth of the inter-zonal part is about 40 mm and the maximum breadth of the shield is estimated at about 130 mm.

In general shape the species is characterized by the broad and flattened cephalic shield, the comparatively narrow inter-zonal part, and the stout cornua. The maximum breadth of the shield is very probably somewhat more than twice as great as the length of the shield in the median line and somewhat greater (or about one and a quarter times as great as) the distance of the tips of the cornua from the rostral end of the shield. From the basis of the cornua the shield rapidly decreases in breadth forwards, and the lateral margins are somewhat convex. The rostral margin is very broad and certainly very obtusely rounded without any rostral angle. There are no angles between the rostral and the lateral margins, the former passing gradually into the latter. The cornua, which are very broad and much flattened dorso-ventrally, project in postero-lateral direction; there is a very slightly marked lateral angle at the transition of the lateral margins of the main shield into those of the cornua. The cornua reach backwards to a point distinctly but not far behind the level of the posterior end of the inter-zonal part. The length of the cornua is contained about twice in the distance of their tips from the rostral end of the shield. The inner margins of the cornua are in the middle of their length provided with few, very small, triangular denticles. In the restorations of the shield by Stensiö (1927, fig. 58) a distinct but very obtuse pectoral angle is shown on the median sides of the cornua. In comparing the figure with the photograph of the shield (pl. 4:1) it is seen that this angle is rather exaggerated in the restoration and in reality very insignificant; it is the very slightly widened median part of the narrow limbus cornualis. The pectoral sinus are very broad and rather deep. The inter-zonal part is rather long, narrow and only slightly decreasing in breadth backwards; its posterior breadth constitutes somewhat less than one-third of the maximum breadth of the shield. The dorsal portion of the inter-zonal part is imperfectly preserved posteriorly but it seems likely that there was no median ridge or crest, and that the posterior angle was only slightly protracted backwards, and not reaching far behind the postero-lateral angles. The dorsal sensory field is about twice as long as broad, broadest in its posterior part and abruptly narrowing in the anterior third of its length; the breadth in the anterior part of the field is only half as great as the breadth in the posterior one; the posterior margin of the field is rounded. The dorsal field has thus about the same shape as in *C. watneliei* (Stensiö 1927, pl. 1:2). The lateral sensory fields are rather narrow in the posterior

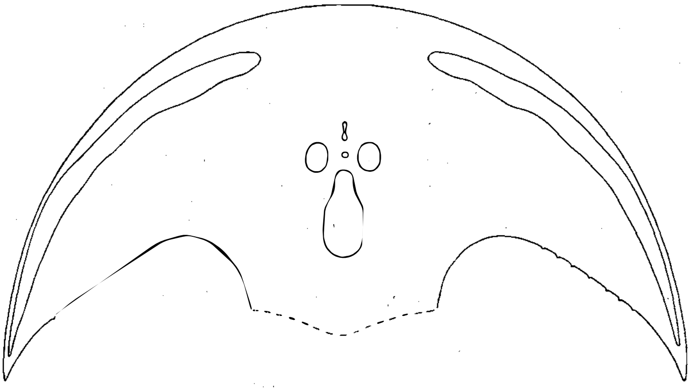


Fig. 68. — *Cephalaspis laticornis* Stensiö. Attempted restoration of the cephalic shield, dorsal view. After ENS nos. 589—590. ⅔.

halves of their length, somewhat widened anteriorly; posteriorly the fields extend on to the distal parts of the cornua and taper slowly and uniformly almost to a point. The orbital openings, which are comparatively small, are situated somewhat in front of the middle of the length of the shield in the median line. The inter-orbital region with the pineal and the naso-hypophyseal openings is not preserved.

The exoskeleton is imperfectly preserved in nos. 589 and 590 but its structure is partly well displayed in no. 591. The superficial layer forms a continuous covering to the middle layer, its outer face is quite smooth. The radiating canals are well developed. In no. 591 it is seen that the radiating canals are arranged in distinct fascicles; the spaces between the fascicles are filled with small irregular canals; the distance between two neighbouring groups of ascending canals is on the average 2.2 mm. The basal layer contains no ringsinus. Very little can be said about the development of the mucous canal system, no large circum-areal canals are, however, observed and it is thus very likely that there is no differentiation into circum-areal and intra-areal canals but that the mucous canal system was lodged in a fine-meshed canal plexus. It must, however, be emphasized that in the holotype the outer parts of the exoskeleton are subdivided into small polygonal areas (Stensiö 1927, p. 256) thus indicating a differentiation of the mucous canal system in circum-areal and intra-areal canals.

The endoskeleton is well preserved only in no. 591, in which the superficial canals have well developed perichondrial bone-layers.

Remarks. — In the general shape of its cephalic shield *C. laticornis* resembles *C. semicircularis* (p. 399) and *C. menoides* (p. 402), and to a certain extent *C. fracticornis* (p. 385), but it cannot be confused with any of these species, being sufficiently well characterized by the shape of the cornua and of the dorsal sensory field; it seems, however, to be more closely related to the two former species than to *C. fracti-*

cornis, from which it is distinguished by a quite different development of the lateral sensory fields.

Geological horizon. — Upper Eodevonian: Wood Bay series, the C. Kjeldsen division.

Localities. — Spitsbergen. E. side of Bock Bay: Mt Kronprinz, W. slope (no. 589); W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier (no. 590); N. of Dickson Bay: Mt Barmfjellet (no. 591).

All the specimens were collected by the ENS expedition in 1939.

48. *Cephalaspis caroli* n. sp.

(Fig. 69; pl. 51.)

1927. *Cephalaspis lata* in part, Stensiö, p. 258; pl. 6:1.

Diagnosis. — A *Cephalaspis* species of large size with maximum breadth of cephalic shield nearly three times as great as length of shield in median line. Shield rapidly narrowing forward. Rostral margin comparatively narrow and rounded, without rostral angle. Lateral margins moderately curved. Cornua long, flat and rather broad, projecting in postero-lateral direction and reaching backwards far behind posterior angle of inter-zonal part. Length of cornua about half as great as distance of their tips from rostral end of shield. Inner margin of cornua without denticles. Pectoral sinus broad and rather shallow. Inter-zonal part broad in proportion to length of shield in median line; posterior breadth of inter-zonal part constituting about one-third of maximum breadth of shield. Dorsal sensory field (probably) short and broad. Lateral sensory fields narrow, reaching far backwards, terminating with pointed ends on distal parts of cornua. Orbital openings situated in front of middle of length of shield in median line. Superficial layer of exoskeleton continuous and smooth. Mucous canal system enclosed in exoskeleton.

Holotype. — Fragmentary cephalic shield (ENS no. 592).

Material. — The material of this species consists of three specimens, ENS nos. 592—593, and Pal. Mus. Oslo no. 10 (D5609). No. 592 (pl. 51:2), the holotype, is represented by a fragmentary and somewhat crushed cephalic shield, lacking most of the left side and a considerable portion of the inter-zonal part as well as parts of the central region. The second specimen (no. 593) consists only of the left cornu with adjacent parts. The third specimen (no. 10; D5609) is a part of the original material of *C. lata* (Stensiö 1927, p. 258; pl. 6:1). An additional specimen (ENS no. 594, pl. 51:1) is placed here with hesitation; it consists mainly of the imperfectly preserved exoskeleton of the dorsal side of a fragmentary shield, lacking most of the anterior

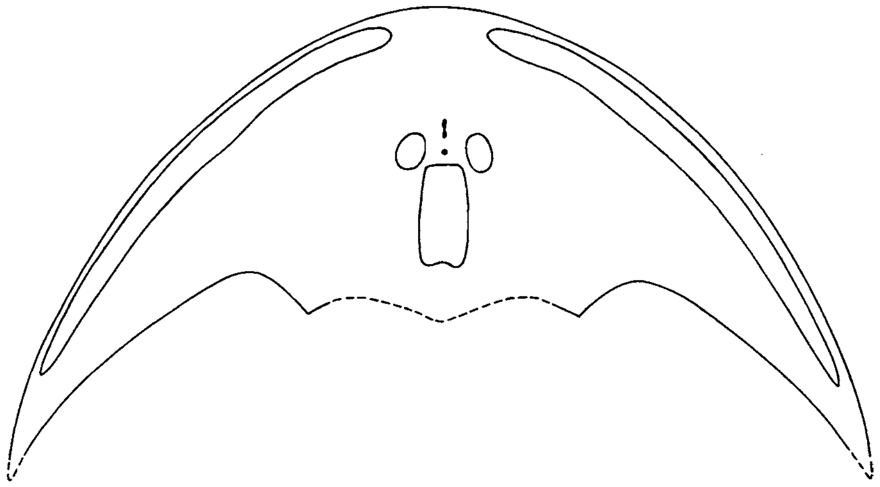


Fig. 69. — *Cephalaspis caroli* n. sp. Restoration of the cephalic shield, dorsal view. Mainly after the holotype (ENS no. 592). ⅔.

portion and the right side; it is furthermore somewhat distorted by pressure of the rock.

Description. — Owing to the imperfect state of preservation of the cephalic shields no exact measurements can be taken. The specimens nos. 10, 592—593 seem to be all of the same size while no. 594, doubtfully placed here, is slightly larger. In the holotype the length of the shield in the median line from the rostral end to the level of the right postero-lateral angle of the inter-zonal part is about 60 mm, and this distance probably corresponds to the real length of the shield in the median line, or is a trifle less than this length; the maximum breadth of the shield, which lies between the posterior ends of the cornua, is estimated at about 170 mm, and the breadth of the inter-zonal part between the postero-lateral angles is probably about 55 mm; the distance of the tips of the cornua from the rostral end of the shield is estimated at about 125 mm; the maximum height of the shield is rather inconsiderable and probably not exceeding 20 mm.

Taken as a whole, the cephalic shield is very broad and short, with a maximum breadth that is almost three times as great as the length in the median line; the distance of the tip of a cornu from the rostral end of the shield is about three-fourths of the maximum breadth of the shield. The shield rapidly decresases in breadth anteriorly. The rostral margin is rather narrow and well rounded but without any rostral angle. The rostral margin passes without interruption of any antero-lateral angles into the lateral margins, which are only moderately curved. The cornua project in a postero-lateral direction and reach backwards far behind the posterior end of the inter-zonal part; they are very long with a length contained about twice in the distance of their tips from the rostral end of the shield. The cornua are furthermore rather broad and flattened dorso-ventrally; their outer margins are slightly rounded. The median margins are almost straight in the basal three-quarters of the length of the cornua, and in dorsal view; in ventral aspect, on the other hand, the inner margins are gently curved; this fact is due to the development of the rather broad cornual shelf. The inner margins of the cornua are devoid of denticles. The pectoral sinus are shallow and rather broad, but of somewhat different shape in dorsal and in ventral view, being somewhat broader and more uniformly concave in ventral than in dorsal aspect. The interzonal part is broad in proportion to the length of the shield in the median line, its breadth being only slightly less than this distance. Compared with the maximum breadth of the shield the breadth of the inter-zonal part is rather small, being contained about three times in it. The inter-zonal part is also very short and rapidly decreases in breadth backwards, its actual shape could not be ascertained as the main parts of it are not preserved; it seems very probable that the height of the inter-zonal part was rather inconsiderable; in no. 594, doubtfully placed here, there is an indication of a low and broad dorsal median ridge. The dorsal sensory field, the shape of which is fairly completely preserved only in no. 594, is here rather short and broad, about one and a half times as long as broad and almost quadrangular in shape; it seems to have about the same shape in no. 592 and no. 593. The lateral sensory fields, which are narrow in proportion to the size of the shield, lie rather near to the lateral borders of the shield; posteriorly they taper gradually and their posterior ends, which lie on the distal third of the cornua, are pointed. The orbital openings, which are of moderate size, are situated in front of the middle of the length of the shield in the median line. The inter-orbital region of the shield is not preserved and therefore nothing is known of the disposition of the pineal and the naso-hypophyseal openings; in no. 594, there is, however, no pineal plate developed.

The oralo-branchial fenestra, the shape of which is partly shown in the specimen figured by Stensiö (1927, pl. 6:1), is about one and a half times as broad as long.

The exoskeleton is rather imperfectly preserved, and its minute structure could thus not be sufficiently well studied. The superficial layer is continuous and its outer face is smooth, without any ornamentation. It is pierced by the very closely set, rather large pores of the mucous canal system which lie in fact so closely that the superficial layer in dorsal view appears as narrow strips in a fine-meshed network. The radiating canals are well developed. No polygonal areas and no circum-areal canals are to be seen, and it is thus very probable that the mucous canal system was not differentiated into circum-areal and intra-areal canals but formed a uniform plexus.

Of the sensory line system only parts of the grooves of the infraorbital line have with certainty been observed.

The endoskeleton seems on the whole to be only weakly ossified; parts of some of the superficial canal layers are seen but as the courses and signification of the canals could not be established, they are not mentioned here.

Remarks. — *C. caroli* was earlier included in *C. lata* (Stensiö 1927, p. 258) but it seems now evident that it cannot pertain to this species. It differs from it by the size and the general shape of the cephalic shield, as well as by the shape and direction of the cornua, and by the comparatively broad inter-zonal part. It is similar to *C. gigas* but its shield is smaller and comparatively shorter with a relatively broader inter-zonal part. *C. caroli* is probably closely related to *C. gigas* and somewhat more distantly to *C. høegi* and *C. lanternaria*. The species is named in honour of Mr. Carl Andreasen, Tromsø, who was a member of the ENS expedition in 1939.

Geological horizon. — Upper Eodevonian: Wood Bay series, the C. Kjeldsen division.

Localities. — Spitsbergen. E. side of West Fiord, between Bryhn Valley and Kaalaas Valley (nos. 592—593, in the same slab); E. side of Bock Bay, Mt Kronprinz, W. slope (the doubtful specimen no. 594). The specimen no. 10 (D. 5609) was found at the inner end of Wood Bay "W. of the Hoffnung Glacier" (Stensiö 1927, p. 259) = Mt Sigurd, on the slope towards the Hoffnung Glacier.

The specimens nos. 592—594 were collected during the ENS expedition in 1939.

49. *Cephalaspis gigas* n. sp.

(Fig. 70; pls. 52—53.)

Diagnosis. — A very large *Cephalaspis* species with maximum breadth of cephalic shield about twice as great as length of shield in median line. Shield rapidly narrowing forwards. Rostral margin more or less convex. Cornua long, rather straight, broad, flattened, projecting in postero-lateral direction and reaching far behind posterior angle of inter-zonal part; their length contained about twice in distance of their tips from rostral end of shield. Inner border of cornua without denticles. Pectoral sinus broad. Inter-zonal part narrow, rather short; its posterior breadth contained about four times in maximum breadth of shield. Dorsal sensory field small, nearly twice as long as broad. Lateral sensory fields narrow, extending backwards to posterior parts of cornua. Orbital openings rather small, situated in front of middle of length of shield in median line. No pineal plate. Exoskeleton with smooth continuous superficial layer. Polygonal areas small in proportion to size of shield, especially in posterior and median parts of shield. Basal layer with ringsinus.

Holotype. — Cephalic shield (ENS no. 597).

Material. — To this species only three specimens (ENS nos. 595—597) are referred with a fair degree of certainty. In addition to these specimens I place here with more or less hesitation four other specimens (ENS nos. 598—601). The holotype, no. 597 (pl. 52), consists of a nearly complete cephalic shield, partly in counterpart, which lacks portions of the rostral and the right lateral borders as well as the very tips of the cornua; it is, furthermore, asymmetrical, being distorted by pressure in the rock. No. 595 (pl. 53) consists mainly of the dorsal exoskeleton of a somewhat crushed and distorted shield. No. 596 consists of a fragmentary cephalic shield, lacking the cornua and a dorsomedian portion of the inter-zonal part. The specimens placed here with hesitation are all represented by very fragmentary cephalic shields, in which only the anterior and portions of the central parts of the shields are preserved to a varying extent.

Description. — The length of the cephalic shield of the holotype in the median line could not be directly measured as the most rostral and posterior ends of the shield are missing, but is estimated at 14.5—15.5 cm; the breadth of the distorted shield between the preserved posterior parts of the cornua is 33 cm but the original breadth of the shield is estimated at about 31 cm; the breadth of the inter-zonal part between the postero-lateral angles is 8.3 cm, and the distance of the pineal foramen from the rostral end of the shield is estimated at 6.9 cm. The height of the shield of the holotype is roughtly estimated at about 3.5 cm. The shield no. 595 is 13 cm long in the median line and the distance of the pineal foramen from the rostral end of the shield is 6 cm. In no. 596 the length of the shield in the median line is estimated at about 14 cm; the breadth of the inter-zonal part between the postero-lateral angles is 9 cm, and the distance of the pineal foramen from the rostral end of the shield is 6.7 cm. The inter-orbital breadth is 2.9 cm in the holotype. The shields referred to this species with hesitation belong all to very large individuals, but only few measurements can be taken, by which the shields can be compared with the preceding ones; thus the distance of the pineal foramen from the rostral end of the shield is 6.9 cm (no. 598), 8.3 cm (no. 599), 8.2 cm (no. 600), and about 8.8 cm (no. 601). In no. 600 the inter-orbital breadth is 2.6 cm.

Taken as a whole the cephalic shield is very large and broad in this species, with a maximum breadth between the tips of the cornua which is about twice as great as the length in the median line, and which is distinctly greater than the distance of the tip of a cornu from the rostral end of the shield; the shield is furthermore rather depressed, with a height that is rather inconsiderable in proportion to the size.

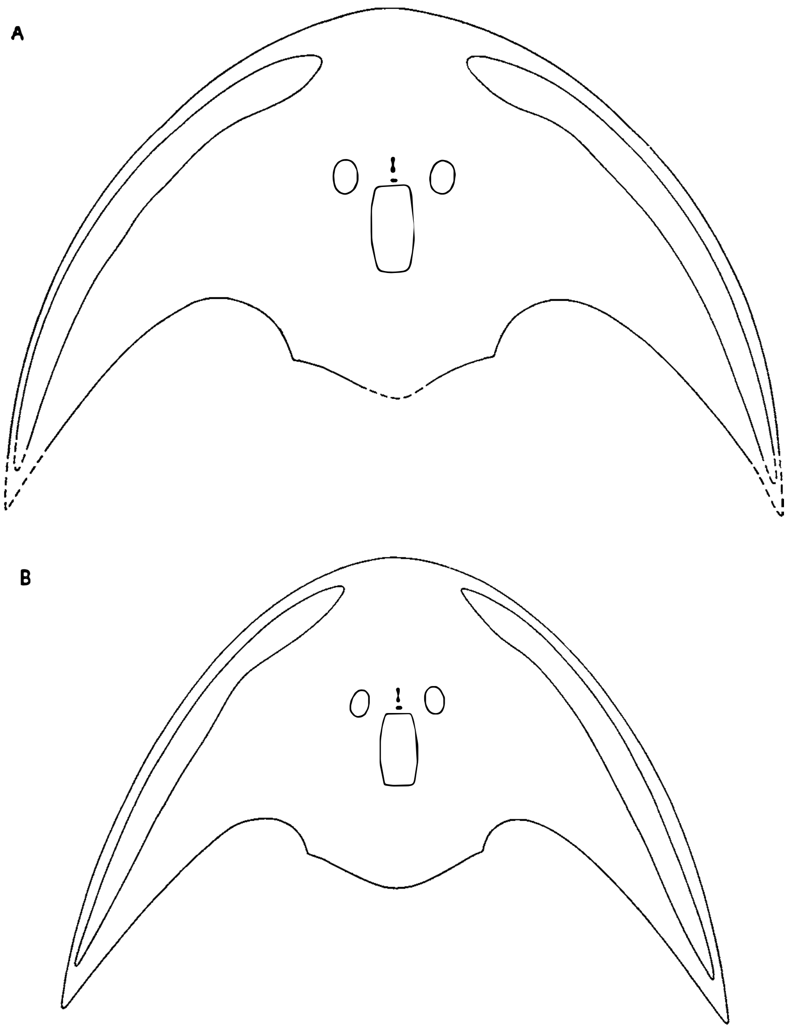


Fig. 70. — *Cephalaspis gigas* n. sp. Restoration of the cephalic shield in dorsal view, A, mainly after the holotype (ENS no. 597), B, after ENS nos. 595. ⅓.

The shield is somewhat variable in shape as is seen from the restorations of two different specimens (fig. 70A, B). The shield rapidly decreases in breadth forwards with rather straight or somewhat convex lateral margin. The rostral margin is moderately broad and more or less curved without any rostral angle. The rostral margin passes imperceptibly into the lateral margins and there are thus no antero-lateral angles. The cornua, which project from the main shield in a postero-lateral direction, are very long and reach backwards far behind the level of the posterior end of the inter-zonal part; their length constitutes somewhat more than half of the distance of their tips from the rostral end of the shield. The cornua are flattened dorso-ventrally and broad in their proximal parts; they are rather straight and taper gradually and uniformly towards their tips; the median margins of the cornua are almost straight. The inner borders of the cornua are devoid of denticles. The pectoral sinus are broad, fairly shallow, and rather uniformly curved. The inter-zonal part is fairly short and comparatively very narrow, narrowing rather rapidly towards the postero-lateral angles; its breadth between these angles is contained no less than about four times in the maximum breadth of the shield. The dorsal portion of the inter-zonal part is imperfectly preserved in the holotype and no. 596, but in no. 595 it is fairly complete although somewhat distorted, and in this specimen there is seen a very indistinct, long, dorsal median ridge. The posterior end of the inter-zonal part is protracted backwards only rather slightly behind the postero-lateral angles, and the posterior angle is obtusely rounded. The sensory fields are fairly small in proportion to the size of the shield. The dorsal field is nearly twice as long as broad, and rectangular in shape with only very slightly curved lateral margins; the anterior and posterior margins are abruptly truncated. The anterior margin of the field lies closely behind the pineal foramen. The distance of the posterior margin of the dorsal field from the posterior end of the shield was very probably nearly one and a half times as great as the length of this field. The lateral sensory fields are narrow, in the posterior parts gently and uniformly tapering towards their ends, which lie near the tips of the cornua. The distance between the antero-median ends of the two lateral fields is about twice as great as the inter-orbital breadth. The orbital openings, which are rather small and oval in shape are situated somewhat nearer to the rostral than to the posterior end of the shield but the distance of an orbital opening from the pectoral sinus of its side is slightly less than its distance from the rostral end of the shield. The inter-orbital breadth is two and a half or three times as great as the transverse diameter of an orbital opening. The antorbital prominences are very slightly indicated. The pineal foramen, which lies between the posterior parts of the orbital openings, is not located in an independent pineal plate. The shape of the naso-hypophyseal opening is not exactly definable as the borders of the opening are imperfectly preserved; at least the middle division is very narrow, and the anterior division, displayed in no. 596, is likewise narrow. The circum-nasal fossa is shallow and very broad, occupying almost the whole interocular space; it is not distinctly bordered posteriorly.

The exoskeleton is rather imperfectly preserved. The outer face of the superficial layer is not well accessible for investigation; it is, however, very probable that it is smooth and without any coarse ornamentation; the superficial layer probably forms a continuous covering to the middle layer between the circum-areal mucous grooves. The middle layer contains radiating canals of very fine calibres. The basal layer is provided with ringsinus, which in the holotype are rather wide. The mucous canal system is not wholly enclosed in the exoskeleton, being located partly in open circum-areal grooves, and partly in intra-areal canals. The polygonal areas, formed by the circum-areal grooves and by the ringsinus, are of somewhat varying sizes. In the holotype comparatively small areas (with an average diameter of 2.5 mm) are often seen, each surrounded by three and four large areas, with an average diameter of 3.7 mm. In no. 595 the polygonal areas near the orbits are very small, about 1.3 mm in diameter, while in other places of the shield they measure 2 mm or more in diameter. In no. 596, where the ringsinus in the basal layer are well displayed, the polygonal areas near the posterior parts of the dorsal sensory field and near the posterior margin of the inter-zonal part are much smaller (about 2 mm in diameter) than in the other regions of the shield (here about 3 mm in diameter). In no. 600, doubtfully placed here, it is obvious that the superficial layer is continuous, and very probably with a smooth outer face; the mucous canal system is not differentiated into circum-areal and intra-areal canals but forms a fine-meshed network; the basal layer is provided with distinct ringsinus, encircling polygonal areas with a diameter of about 4 mm or even more.

The endoskeleton seems to be fairly well ossified in the holotype but is not well exposed for observation; in no. 595 and no. 596 as well as in the specimens, doubtfully placed here, rather little or nothing is preserved of the internal structures.

Remarks. — *C. gigas* is characterized by its very large size, its broad cephalic shield, the comparatively very narrow inter-zonal part, as well as by the shape and direction of the cornua. It resembles rather much *C. caroli* (p. 408) but differs from that species by the greater size, the narrower and longer inter-zonal part, and by the somewhat differently shaped cornua.

There exists a slight possibility that *C. gigas* is specifically identical with the equally-sized *C. lata* (Stensiö 1927, p. 258). With regard to this latter species it may be noted here that with the species concept used in this paper, *C. lata* includes only the holotype (Pal. Mus. Oslo no. 10, Stensiö 1927, p. 258, pl. 7), while the other specimen (Pal. Mus Oslo no. 9) referred to the species by Stensiö is here placed in the new species *C. caroli*. The holotype specimen consists of a rather imperfect cephalic shield, exposed from the ventral side, and probably distorted by pressure of the rock; the characters occurring on the dorsal side of the shield are thus unknown and the real shape of the shield is uncertain, and on account of these facts it will probably be very difficult in the future to recognize the species with any certainty. In comparing *C. gigas* with *C. lata* we have thus only very few points of comparison to look for. There are, however, some details which are differently developed in the two species and which may indicate a specific differentiation, viz. the shape of the rostral margin, and the shape and direction of the cornua. *C. gigas* is also probably very similar to *C. høegi* (Stensiö 1927, p. 260), but also this species is too imperfectly known as to allow of a closer comparison. *C. gigas* seems to differ from it by the larger size of the shield, by the broader shield, and probably by the direction of the cornua. From *C. lanternaria* which is of about the same size as *C. gigas,* it differs mainly by the more obtusely rounded rostral margin, the narrow inter-zonal part, and the longer cornua.

The specimens placed here with hesitation resemble the holotype rather closely in the general shape of their preserved parts but as the shields are very incomplete, and nothing can be said about the real shape of the complete shields, and as there are some differences i. a. in the structure of the exoskeleton, they may possibly pertain to closely related species, and are therefore placed here only provisionally.

Geological horizon. — Upper Eodevonian: Wood Bay series, the C. Kjeldsen division (? the Lyktan division).

Localities. — Spitsbergen. N. of Dickson Bay: Mt Barmfjellet (no. 597). E. side of Wood Bay: Mt Wächter, slope towards Wood Bay (nos. 595—596). The localities for the specimens doubtfully placed here are the following: N. of Dickson Bay: Perched Block Mtn (nos. 598—599). E. side of Dickson Bay: Mt Rebbingen (= "the Mt. N. of Fiskedalen"), S. W. slope (no. 600). E. side of Wood Bay: Mt Scott Keltie, S. part, W. slope (no. 601).

All the specimens were collected during the ENS expedition in 1939.

50. *Cephalaspis lanternaria* n. sp.

(Fig. 71; pl. 54.)

Diagnosis. — A very large *Cephalaspis* species with maximum breadth of cephalic shield nearly one and three-quarter times as great as length of shield in median line. Shield rapidly narrowing forward. Rostral margin narrow, sharply rounded, without rostral angle. Lateral margins slightly curved. Cornua rather broad and stout, projecting in postero-lateral direction and reaching backwards somewhat farther than posterior angle of inter-zonal part; their length contained about two and a half times in distance of their tips from rostral end of shield. Outer border of cornua rather convex, inner border almost straight, without denticles. Pectoral sinus moderately broad and deep. Inter-zonal part rather broad and short, its breadth posteriorly contained about two and a half times in maximum breadth of shield. Dorsal sensory field rather short and broad, one and a half times as long as

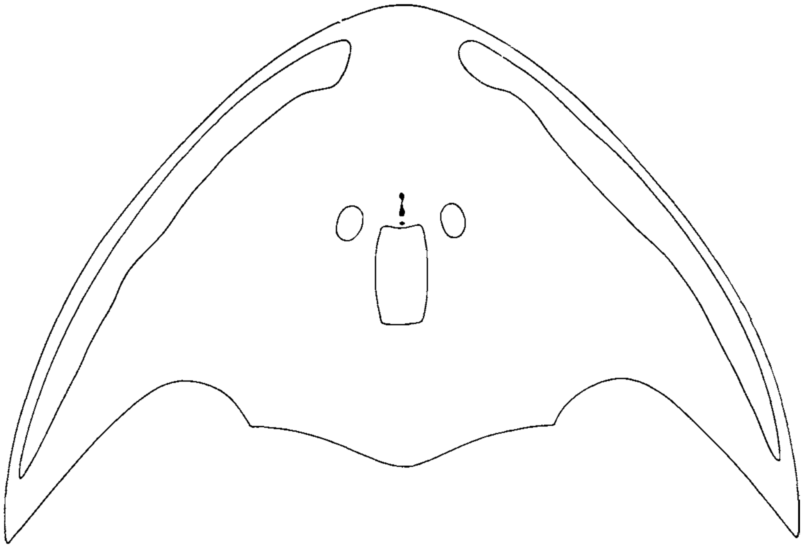


Fig. 71. — *Cephalaspis lanternaria* n. sp. Restoration of the cephalic shield in dorsal view. After the holotype (ENS no. 602). ⅓.

broad, anterior and posterior margin truncated. Lateral sensory fields tapering gently backwards, extending on to distal third of cornua. Orbital openings small, situated slightly before middle of length of shield in median line. No pineal plate. Outer face of exoskeleton smooth. Basal layer with ringsinus. Mucous canal system developed as uniform plexus.

Holotype. — Cephalic shield (ENS no. 602).

Material. — The material referable to this species consists of three specimens (ENS nos. 602—604). The holotype (no. 602, pl. 54), is represented by an almost complete cephalic shield in counterpart, no. 603 by the right side of a cephalic shield, much compressed laterally; no. 604 consists of part of the dorsal exoskeleton (exposed in ventral view) of a very incomplete shield lacking i. a. the cornua and most of its right side, and is furthermore rather much distorted. One additional specimen (ENS no. 605), placed here with hesitation, consists only of the left cornu and some adjacent parts.

Description. — The holotype shield (no. 602) has the following dimensions. The length in the median line is about 18 cm, and the maximum breadth, which lies between the tips of the cornua, is about 31 cm; the distance of the tips of the cornua from the rostral end of the shield measures between 26 and 27 cm. The breadth of the interzonal part between the postero-lateral angles amounts to 11 cm, and the distance of the pineal foramen from the rostral end of the shield to 8.8 cm. The inter-orbital breadth is about 3.5 cm. The height of the shield could not be measured, it is, however, estimated at somewhat more than 5 cm. The other two specimens are of about the same size as the holotype, but very few comparable measurements can be taken on them; in no. 603 the distance of the tip of the cornu from the rostral end of the shield is about 24.5 cm, and the distance of the pineal foramen from the rostral end is estimated at 9 cm; in no. 604 the latter distance is estimated at 8.5 cm. As is seen from the measurements, the species must have attained a very large size.

In general appearance the cephalic shield is characterized by its large size and triangular shape, with a maximum breadth which is about one and three-quarter times as great as the length in the median line and distinctly greater than the distance of the tip of a cornu from the rostral end of the shield. The shield rapidly narrows anteriorly with slightly curved lateral margins. The rostral margin of the cephalic shield is narrow and rather strongly convex but without any distinct rostral angle; there are no angles at the transition between the rostral and the lateral margins but the former passes imperceptibly into the latter. The cornua, which are stout, broad and flattened dorso-ventrally but only moderately long, project in postero-lateral direction; they reach backwards for some distance behind the posterior end of the main shield. The length of the cornua is contained about two and a half times in the distance of their tips from the rostral end of the shield. The lateral margins of the cornua are somewhat convex, whereas their median margins are almost straight; the inner borders of the cornua are devoid of denticles. The pectoral sinus are moderately broad and deep, and uniformly concave. The inter-zonal part is comparatively short, and decreasing in breadth towards its postero-lateral angles; the breadth between them is, however, rather great, constituting about two-fifths of the maximum breadth of the shield. The posterior angle which is very obtuse and rounded is protracted only slightly behind the postero-lateral angles. The dorsal face of the inter-zonal part is not exposed in any of the specimens and it is thus impossible to say anything about its configuration, whether there is a dorsal spine or not. The height of the inter-zonal part is rather considerable, being at least half as great as the breadth of the inter-zonal part. The dorsal sensory field is fairly small compared with the large size of the shield; it is about one and a half times as long as broad and its lateral margins are only slightly curved, the posterior and anterior margins are truncated, the latter being slightly concave; it lies closely behind the pineal foramen. The distance of the posterior margin of the field from the posterior end of the shield is about one and a half times as great as the length of the field. The lateral sensory fields are rather narrow and situated near to the lateral margins of the shield; behind their most anterior parts they are somewhat constricted. Slightly behind the level of the orbits the lateral fields narrow slightly but rather abruptly, and from this point and backwards the fields taper very gently and uniformly, reaching backwards to the distal third of the cornua. The distance between the antero-median ends of the two lateral fields is slightly greater than the inter-orbital breadth. The orbital openings, which are small in proportion to the size of the shield, lie rather far apart and are situated somewhat nearer to the rostral than to the posterior end of the shield; they are oval in shape with their main axes slightly converging anteriorly, and surrounded by a fairly thick circum-orbital ridge. The antorbital prominence is rather small. The pineal foramen is not placed in an independent pineal plate. The naso-hypophyseal opening is rather narrow with fairly indistinctly marked anterior and posterior divisions. The circum-nasal fossa is broad and shallow and indistinctly delimited.

The exoskeleton is rather imperfectly preserved; in the main parts of the shield it is very thin, only the basal layer is more strongly developed in the posterior parts of the shield (especially on the cornua and along the lateral borders of the dorsal sensory field, but also in the circum-orbital ridge and anteriorly to the orbits) than in the anterior parts of the shield. The outer face of the exoskeleton is quite smooth without any ornamentation. It could not be ascertained whether the superficial layer is present or not in the spaces between the mucous grooves. The middle layer is extremely thin. In some places vascular canals of very fine calibres have been observed, evidently corresponding to the radiating canals, but not clearly observed to form regular vascular areas. The basal layer contains rather wide ringsinus, encercling polygonal areas of rather variable sizes; their average diameter is estimated at 3.2 mm. The mucous system was not enclosed in the exoskeleton; it was developed as a regular, rather fine-meshed network, located in open grooves.

The endoskeleton is rather poorly preserved; only some traces are seen of the canal layers as well as parts of the inter-zonal endoskeleton.

Remarks. — *C. lanternaria* is distinguished from its congeners by the general shape of its shield and by the rather broad and fairly high inter-zonal part together with the stout cornua. It is probably closely akin with *C. høegi* (Stensiö 1927, p. 260), *C. gigas* (p. 411) and *C. caroli* (p. 408). It differs from them all by the narrow rostral end of its shield, and by the comparatively broad inter-zonal part, from *C. caroli* and *C. gigas* furthermore by the rather short cornua and from *C. caroli* and *C. høegi* by the greater size of its shield. It is also somewhat similar to *C. magnifica* (Stensiö 1932, p. 142) from the Middle Devonian of Scotland but this species is too imperfectly known as to allow a closer comparison to be made; both species are of about the same size but *C. lanternaria* seems to broader, and to have differently shaped cornua and dorsal sensory field.

Geological horizon. — Upper Eodevonian (?): Wood Bay series, the Lyktan division.

Localities. — Spitsbergen. E. side of Dickson Bay: Mt Lyktan, S. E. slope (towards the Nathorst Valley; nos. 602—603, on the same slab; no. 604), S. W. slope (no. 605, doubtfully placed in this species).

All the specimens were collected by the ENS expedition in 1939.

Species previously known from Spitsbergen, but not found in the present material.

The following *Cephalaspis* species, previously described from Spitsbergen, have not been recognized in the new material now at hand. I have had the opportunity of seeing all the specimens, belonging to them, in the Palaeontological Museum of Oslo.

Cephalaspis watneliei Stensiö.

1927. *Cephalaspis watneliei,* Stensiö, p. 247; fig. 53; pl. 1:1.

Holotype. — Cephalic shield (no. 1) in the Palaeontological Museum, Oslo.

Remarks. — Of this species only a single specimen is known. The species, which was of a medium size, is fairly easily recognized, especially by the distinct rostral angle on the cephalic shield, the very short inter-zonal part and the shape of the dorsal sensory field. It does not seem to be very closely allied to any of the *Cephalaspis* species, hitherto known.

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, the lower part of the C. Kjeldsen division.

Cephalaspis borealis Stensiö.

1927. *Cephalaspis borealis,* Stensiö, p. 248; fig. 54; pl. 1:3.

Holotype. — Fragmentary cephalic shield (no. 2) in the Palaeontological Museum, Oslo.

Remarks. — This species is only represented by a fragment of a cephalic shield, and the missing part of the shield cannot be restored with any accuracy. The species can possibly be recognized by the large size of its cephalic shield, the long, rather pointed, posteriorly directed cornua and the narrow dorsal sensory field. It will be noted here, that the lateral sensory fields, which are narrow, lie near to the lateral margins of the shield, and extend backwards to a point on the distal parts of the cornua only somewhat before their tips. In this respect the species resembles several other *Cephalaspis* species from the Wood Bay series, i. e. *C. oblonga* (p. 393), *C. producta* (p. 390), *C. caroli*

(p. 408), *C. moy-thomasi* (p. 396), *C. semicircularis* (p. 399), *C. menoides* (p. 402), *C. laticornis* (p. 405), *C. gigas* (p. 411), and *C. lanternaria* (p. 416); it is probably closely related to them, possibly most intimately to *C. moy-thomasi.*

Geological horison. — Upper Eodevonian?: Wood Bay series.

Cephalaspis acuticornis Stensiö.

1927. *Cephalaspis acuticornis,* Stensiö, p. 251; fig. 56; pl. 2:4.

Holotype. — Fragment of cephalic shield (no. 55) in the Palaeontological Museum, Oslo.

Remarks. — The species is known only from a postero-lateral fragment of a cephalic shield. The shape of the major part of the shield is unknown, and it will, in fact, be very difficult to identify the species again. For this reason, the shape of the inter-zonal part with a distinct dorsal median ridge and the rather broad, posteriorly rapidly tapering, lateral sensory fields, must be included among the characteristic features. The peculiar shape of the pectoral sinus in the type specimen, on the other hand, seems to be due to an imperfect preservation of this region of the shield.

Geological horizon. — Upper Eodevonian?: Wood Bay series.

Cephalaspis lata Stensiö.

1927. *Cephalaspis lata,* Stensiö, p. 258; fig. 60; pl. 7 (not pl. 6:1).

Holotype. — Cephalic shield (no. 9) in the Palaeontological Museum, Oslo.

Remarks. — Of the two specimens referred to this species in the original description, one is in this paper transferred to the new species *C. caroli* (p. 408).

Based on a badly preserved specimen, the species is very imperfectly known, and can probably not be recognized. There is, however, some possibility that *C. lata* and the new species *C. gigas* might be conspecific (see p. 415).

Geological horizon. — Upper Eodevonian?: Wood Bay series.

Cephalaspis høegi Stensiö.

1927. *Cephalaspis höegi,* Stensiö, p. 260; fig. 61; pl. 8; ? pls. 9—10 (not figs. 62—63).

Holotype. — Cephalic shield (no. 11) in the Palaeontological Museum, Oslo.

Remarks. — The species was based on a fragmentary cephalic shield. Two other shields were placed in the same species with some doubt; one of these shields (no. 115; Stensiö 1927, figs. 62—63) does certainly not belong here, and is indeterminable.

C. høegi is probably closely related to *C. gigas* (p. 411) and *C. lanternaria* (p. 416), described in this paper.

Geological horizon. — Upper Eodevonian?: Wood Bay series, the Lyktan division.

Cephalaspis spitsbergensis Stensiö.

1927. *Cephalaspis spitsbergensis,* Stensiö, p. 276; fig. 70; pl. 33:1 (not fig. 71; pls. 35:3; 39; 40:2).

Holotype. — Fragmentary cephalic shield (no. 58) in the Palaeontological Museum, Oslo.

Remarks. — This species is based on a very badly preserved and much distorted cephalic shield. In the size, the long cornua and the rather long inter-zonal part it is suggestive of the new species *C. signata* (p. 347) but as we know very little about *C. spitsbergensis* we have no idea of the real shape of its shield and cannot carry out a closer comparison between the two species. *C. spitsbergensis* can probably not be recognized.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Ben Nevis division.

Cephalaspis gracilis Stensiö.

1927. *Cephalaspis gracilis,* Stensiö, p. 279; fig. 73; pl. 38:2-3.

Holotype. — Cephalic shield (no. 65) in the Palaeontological Museum, Oslo.

Remarks. — The species is very imperfectly known, and nothing can be said about its relation to the other species of the genus. In the general outline of its shield, the species is somewhat reminiscent of *C. signata* (p. 347).

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Ben Nevis division.

Cephalaspis apicalis Stensiö.

1927. *Cephalaspis apicalis,* Stensiö, p. 282; pl. 37:3 (not pl. 40:4).

Holotype. — Cephalic shield fragment (no. 75) in the Palaeontological Museum, Oslo.

Remarks. — The species is based only on a small rostral fragment of a cephalic shield. The second specimen (no. 76) provisionally placed in the same species, very probably does not belong here but represents a different species, as also suggested by Stensiö.

The species is said to be characterized by the somewhat protracted rostral end of the shield. This character the species, however, shares with other *Cephalaspis* species from Spitsbergen, viz. *C. acuminata*

(p. 258), *C. eurhynchus* (p. 262), *C. føyni* (p. 265), *C. broughi* (p. 268), and *C. deltoides* (p. 271). It cannot be the same species as any of these with the possible exception of *C. deltoides,* but the identity of the two species cannot be proved with any certainty whatever. *C. apicalis* is preferably put aside as a dubious species, which cannot be recognized.

Cephalaspis specimens indeterminable as to species.

Both from the Red Bay and the Wood Bay series there are many fragments, either quite indeterminable or not complete enough to be described adequately as new species. In the following pages only a few of them are treated, which belong to or are supposed to belong to the genus *Cephalaspis,* and which are of some interest from an anatomical, systematical or stratigraphical point of view.

Specimen ENS no. 606 (pl. 55:1). This specimen consists of a fragmentary and somewhat crushed cephalic shield. The shield is very large and was probably at least 26 cm broad; the inter-orbital breadth is 21.3 mm, and the dorsal sensory field is 37.5 mm long. The maximum breadth of the shield was probably at least twice as great as the length in the median line. The cornua, which are directed in a postero-lateral direction, are very strongly developed and constituted a major part of the shield. The inner margins of the cornua are provided with a rather broad cornual shelf, which has some rather sparse, very small, posteriorly or postero-medially directed denticles, and in this respect somewhat recalls that of *C. laticornis.* The lateral sensory fields lie near to the lateral margins of the shield. The pineal foramen is situated in a deep sinus in the anterior margin of the dorsal sensory field and is not lodged in an independent pineal plate. The exoskeleton is subdivided into polygonal areas. The ornament of the outer face of the exoskeleton consists in each polygonal area of six or seven centrally placed rather small tubercles and, surrounding them, there is a greater number of yet smaller tubercles; some scattered small tubercles are often seen lying in the grooves between the polygonal areas. This specimen represents without doubt a new species, which probably is related to *C. laticornis, C. gigas* and its allies.

Locality. — Spitsbergen. W. side of Wood Bay: Mt Kronprinz, opposite the Stjørdalen Valley (Wood Bay series, upper part of the C. Kjeldsen division).

Specimen ENS no. 607 (pl. 55:2) consists of the imperfect rostral and lateral parts of a very large cephalic shield exposed in ventral view. The shield is somewhat distorted by pressure in the rock. The breadth between the tips of the cornua is estimated at about 24 cm and the length of the shield from the rostral end to the level of the pectoral sinus is about 22 cm. The most remarkable character is found in the very small cornua, their length being contained about eight times in the distance of their tips from the rostral end of the shield; they are thus comparatively much smaller than in *C. brevicornis* or *C. lornensis.* This specimen represents a new species.

Locality. — Spitsbergen. E. side of Wood Bay: Mt Scott Keltie, S. part, W. slope (Wood Bay series, ? the C. Kjeldsen division).

Specimen Pal. Mus. Oslo no. A30098 (pl. 58:1) consists of a fairly complete cephalic shield, lacking parts of the cornua; it is distorted by pressure in the rock. The shield is small; its length in the median line is 19.7 mm and its maximum breadth is estimated at about 21 mm. In the general shape of its shield this specimen is similar to *C. exilis* but as the shield is distorted and imperfect it is difficult to make closer comparisons. The shield narrows forwards much as in *C. exilis;* the pectoral sinus have the same general shape as in *C. exilis* and its allies; the cornua are very imperfectly preserved, their length seems to have been contained slightly more than three times in the distance of their tips from the rostral end of the shield; it could not be ascertained whether the inner margins of the cornua are provided with denticles or not. The inter-zonal part is apparently somewhat broader than in *C. exilis* but is otherwise of a shape similar to this species. Nothing definite is known of the shape of the sensory fields nor of the structure of the exoskeleton. It seems possible that the species, represented by this specimen, is related to *C. exilis* and its allies, but on account of our insufficient knowledge of it nothing definite can be said in this matter. The specimen is noted here because it comes from the middle parts of the Wood Bay series and here represents a special *Cephalaspis* type very rare in these layers but common in the Red Bay series.

Locality. — Spitsbergen. W. side of Wijde Bay (West Fiord): Mt Errol White (= "the mountain S. of the Sneugle Valley"). Wood Bay series, the Lyktan division. Collected by Th. Vogt's expedition in 1928.

Specimen ENS no. 609 (pl. 58:2) consists only of the central part (the surroundings of the orbital openings and the anterior part of the dorsal sensory field) of a very large cephalic shield. The interorbital breadth is no less than 5.5 cm and if we may draw any conclusions from this measurement as to the size of the shield this must have been considerably larger than the shields even of *C. gigas, C. lanternaria* and *C. magnifica.* The orbital openings are surrounded by a broad circum-orbital ridge. There is no pineal plate. An opening between the orbital openings in the median line on a small elevation in a wide circum-nasal fossa may represent the nasal opening and if this be true the nasal opening was separated from the opening for the hypophyseal duct (which is not preserved in the specimen), or it may represent the entire very small naso-hypophyseal opening. The exoskeleton is ornamented with numerous groups of comparatively small tubercles, each group including five to eleven or more, mostly about seven, tubercles of which the central tubercle is often somewhat larger than the others. The spaces between the groups of tubercles very probably correspond to the circum-areal grooves of the mucous canal system. This specimen certainly represents a new species. If it really pertains to *Cephalaspis* (which is not proved at all) this is the geologically youngest form of *Cephalaspis* known from Spitsbergen and along with *Acrotomaspis* sp. 2 the only Cephalaspid known from the Grey Hoek series.

Locality. — Spitsbergen. W. side of Wijde Bay: the Sixth Valley (Sjettedalen). Grey Hoek series.

Specimen ENS no. 608 (pls. 59:1; 60). The specimen consists of the left side of a cephalic shield, in counterpart; the most median parts are missing. The shield must have measured somewhat more than 74 mm (which is the length of the preserved median part of the shield) in median line. It is not possible to obtain an idea of the real shape of the shield and of the orbital openings, the dorsal sensory field, the dorsal spine, if present, etc. The shield is mentioned here and in the general part of this paper because it exhibits rather beautifully the dorsal superficial canals in the visceral and zonal endoskeleton.

Locality. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Anglaspis horizon (Red Bay series).

Specimen ENS no. 610 (pls. 56—57) consists of the central and posterior parts of a fairly small cephalic shield. The distance of the pineal foramen from the posterior end of the shield is 22 mm; the breadth of the inter-zonal part is estimated at about 26 mm. The dorsal sensory field is rather short and broad. The inter-zonal part, which is fairly long, is provided dorsally with a moderately high, vertical, dorsal spine. A similar shape of the dorsal spine is not found in any of the described *Cephalaspis* species, with the possible exception of *C. websteri,* to which the present specimen cannot pertain, and it seems thus most probable that it represents a new species. The endoskeleton is well ossified and the shield has been cleaned in such a way that it i. a. shows the inner aspect of the cranial cavity.

Locality. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the Anglaspis horizon, found in the same block as *C. hastata* (Red Bay series).

Specimen ENS no. 611 (pl. 59:2). This specimen consists only of an imperfect dorsal spine of which the distal part is missing. The endoskeleton reaches far upwards into the spine and exhibits very well strongly developed superficial vein canals.

Locality. — Spitsbergen. E. side of Red Bay: the Andrée Glacier, S. half, W. part, in the moraine (Red Bay series).

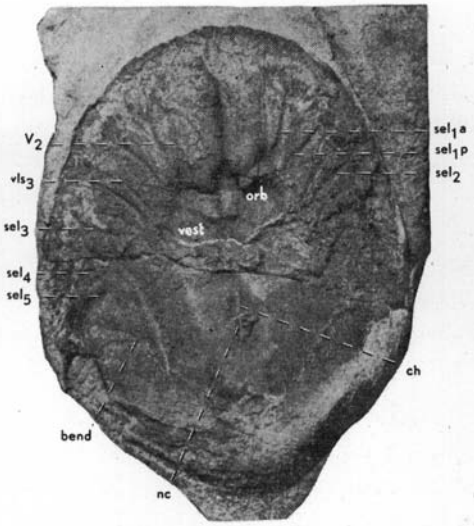


Fig. 72. — *Cephalaspis* sp. Somewhat imperfect and much abraded cephalic shield in dorsal view (Pal. Mus. Oslo no. A30099). About × 1½.

bend, posterior border of the endoskeleton; *ch,* canal for the notochord; *nc,* neural canal; *orb,* orbit; sel_1a, sel_1p, branches of the first nerve canal for the lateral sensory field; sel_2—sel_5, second to fifth nerve canals for the lateral sensory field; *vest,* vestibulum; vls_3, canal for the third dorso-lateral superficial vein; V_2, canal for the r. maxillaris trigemini.

Specimen Pal. Mus. Oslo no. A30099 (fig. 72). This specimen consists of a cephalic shield, which lacks some of its lateral parts including most of the cornua and is furthermore very much worn and abraded. The shield is rather small, measuring 35 mm in median length; the maximum breadth of the shield in its actual state of preservation is 33 mm and the original maximum breadth is estimated to have been only slightly greater; the posterior breadth of the inter-zonal part is 22.5 mm. The shield has thus been about as long as broad or only slightly broader than long. It is slightly narrowing forwards and the rostral margin is very broad and obtusely rounded. The cornua are evidently projecting in a straight posterior direction and they were very probably rather small. The pectoral sinus are fairly deep and very narrow. The inter-zonal part is very broad and its breadth is probably about two-thirds of the maximum breadth of the shield. The lateral sensory fields extend backwards on to the cornua. The nerve canal sel_1 is disposed and subdivided in the same manner as in the typical *Cephalaspis* species. The exoskeleton is preserved only in small patches on the shield; its outer face is quite smooth without any ornamentation. The middle layer has well developed radiating canals. The mucous canal system seems to form a uniform plexus; the pores of the mucous canals in the superficial layer are very small and closely set.

This specimen certainly represents a new species, which is characterized by its stout cephalic shield with broad rostral margin, broad inter-zonal part and probably small, posteriorly directed cornua. In the general shape of its shield the species rather much resembles *Thyestes salteri* (Egerton) but it is evidently a true *Cephalaspis* species. Among the *Cephalaspis* species it bears some resemblances to *C. lornensis* (Traquair 1899a; Stensiö 1932, p. 118), *C. eurynotus* (p. 320) and *C. sinuata* (p. 334) but it is much smaller and the shield does not narrow forwards so much as in these species. The specimen is mentioned here because it is one of the two Cephalaspids (the other one being *C. corystis),* which are found in the lowest fossiliferous layer (the "Psammosteus" horizon) in the Spitsbergen Old Red.

Locality. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, in the "Psammosteus" horizon (Red Bay series). Collected in 1928 by Th. Vogt's expedition.

Genus **Securiaspis** Stensiö.

1927. *Cephalaspis* in part, Stensiö, pp. 246, 272—275.
1932. *Securiaspis,* Stensiö, p. 159.

Diagnosis. — A cephalaspid genus with broad, depressed cephalic shield. Cornua well developed, extending backwards about as far or well behind posterior end of inter-zonal part. Pectoral sinus well defined, broad and rather deep. Inter-zonal part fairly long and narrow, usually with distinct dorsal median ridge and slightly protracted posterior angle; postero-lateral angles not protracted and posterior margin not emarginate. Sensory fields well developed, consisting of one unpaired dorsal and one pair of lateral fields; lateral fields extending backwards on to basal parts of cornua, without any distinct postero-median angle towards zonal part proper. Orbital openings generally situated rather far backwards, nearer to posterior than to rostral end of shield. No pineal plate. First nerve canal of lateral sensory field undivided until somewhat antero-laterally to orbit, and occasionally almost as far as to lateral sensory field. Canal for r. mandibularis trigemini very long, passing down to oralo-branchial chamber entirely behind first nerve canal of lateral sensory field or between its two branches. Canal for third dorso-lateral superficial vein opening into postero-dorso-lateral corner of orbit or directly into canal for vena capitis lateralis closely behind orbit. Middle layer of exoskeleton of cephalic shield with well-developed radiating canals. (After Stensiö 1932, p. 159; somewhat modified.)

Type species. — *S. kitchini* Stensiö (original designation, Stensiö 1932, p. 159).

Remarks. — The diagnosis given above is taken from Stensiö (1932, p. 159) but altered in accordance with the new facts brought to light by the study of the new species described below and with the transfer of *Cephalaspis staxrudi* Stensiö to this genus. The probability of this species being in reality a *Securiaspis* is already suggested by Stensiö (1932, p. 160, see also Säve-Söderbergh 1941b, p. 239, note), and the new material of this species at my disposal shows clearly that this presumtion was well founded (it has recently been definitely referred to *Securiaspis* by Denison, 1951a, pp. 159, 191).

With regard to the diagnosis given by Stensiö it may be convenient here to make some remarks. It is interesting to note that the proximal course of the canal vls_3 is not constant in the different species. In *S. kitchini* (Stensiö 1932, pl. 49:1) the canal in question joins the canal vls_4 and the common trunk thus formed runs on to and opens into the canal *vcl* somewhat behind the orbit; in a specimen of *S. staxrudi* (pl. 62:1), the common trunk possibly received an additional canal (vls_5) and then runs to the most posterior part of the orbit in such a way that it opens with its anterior half into the orbit and with its posterior half into the canal *vcl;* in *S. quadrata* the canal vls_3 behaves in a similar way. In *S. kingi* (Stensiö 1932, pl. 49:2) the canal vls_3 seems to open into the postero-dorso-lateral corner of the orbit; in an undetermined *Securiaspis* specimen, described below, it opens clearly into the orbit (pl. 63:2). It may be added that the canal *vcl* issues from the most posterior part of the orbit and runs backwards, curving slightly medially; it has thus a very median position.

In this connection must also be noted the different disposition of the branches of the first nerve canal for the lateral sensory field on each side in the holotype of *S. kitchini* (Stensiö 1932, p. 161; pl. 49:1), the conditions on the right side being typical for the genus, but on the left side quite as in *Cephalaspis.* That part of the canal V_3, which enters the dorsal face of the endoskeleton, runs on the right side entirely behind the canal sel_1, but on the left side between the two branches of this canal.

A feature, which distinguishes the genus *Securiaspis* from *Cephalaspis,* is the long portion of the canal V_3 situated superficially in the visceral endoskeleton.

Stensiö (1932, pp. 151—152, 159) refers *Securiaspis* to his subfamily "Kiaeraspinae" and within this to the same group of genera as *Benneviaspis, Hoelaspis, Boreaspis* and *Kiaeraspis,* and he considers it as most akin to *Benneviaspis.* In the general shape of the cephalic shield the genus certainly reminds most closely of *Benneviaspis* among the genera just mentioned, but there are also several important differences between the two genera, e. g. the different shape of the inter-zonal part and of the lateral sensory fields, and the affinities between the two genera cannot be very close. As is shown in the remarks on the family Cephalaspididae the assumed differences between the subfamily "Cephalaspinae" and the first genus group of "Kiaeraspinae" are of no real systematic value, and the separation of *Securiaspis* and *Cephalaspis* in two different subfamilies is not justified. *Securiaspis* shows in fact a very close resemblance to *Cephalaspis,* and as seen from the diagnoses of the two genera, they are not at all very clear-cut. As, however, *Securiaspis* includes species of a distinct habitus of the cephalic shield and as they very probably are closely related to each other, they are, at least provisionally, separated from *Cephalaspis* and kept in a genus of their own.

The genus *Securiaspis* contains at present the following species, viz. *S. kitchini* Stensiö and *S. kingi* Stensiö from the Dittonian of England, *S. staxrudi* (Stensiö) and *S. quadrata* n. sp. and (at least one) unnamed species (see remarks to *S. staxrudi,* p. 432; and also p. 435) from the Red Bay series of Spitsbergen. With regard to *S. kingi* it must be observed that this species is rather imperfectly known and that its place in *Securiaspis* is by no means clearly established. It can furthermore be noted that the occurrence of the genus in the Old Red layers of Podolia has been established by Zych, according to a specimen determined by him, which I have seen.

1. *Securiaspis staxrudi* (Stensiö).

(Fig. 73; pls. 61—62; 63:1; 65:2.)

1927. *Cephalaspis staxrudi* in part, Stensiö, p. 272; fig. 68; pl. 37:1 (not fig. 69; pls. 34; 36:4).

Diagnosis. — A *Securiaspis* species of medium size with maximum breadth of cephalic shield about or somewhat more than one and a half times as great as length of shield in median line. Shield more or less narrowing forwards. Rostral margin broad, rather obtusely rounded without rostral angle; lateral margins curved. Cornua very long and slender, projecting in posterior direction, extending backwards far behind level of posterior angle of inter-zonal part; inner margins without denticles. Length of cornua contained about twice in distance of their tips from rostral end of shield. Pectoral sinus deep. Inter-zonal part fairly narrow; its posterior breadth constituting somewhat more than one-third af maximum breadth of shield. Dorsal sensory field about two and a half times as long as broad, with truncated anterior and convex posterior margin. Exoskeleton ornamented with small elongate tubercles.

Holotype. — Cephalic shield (no. 56) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 272).

Material. — The new material at my disposal comprises nine more or less fragmentary cephalic shields, Pal. Mus. Oslo nos. A30015 (pl. 61), A30016, A30017 (pl. 63:1), A30018—A30019, A30020 (pl. 62:1), A30021 (pl. 65:2) and ENS nos. 485, 486 (pl. 62:2). One very fragmentary and crushed shield (Pal. Mus. Oslo no. A30022) is placed with hesitation in this species.

Description. — The dimensions of the cephalic shields in mm are collected in the following table (figures in brackets are only approximate):

Nos.	485	486	A30015	A30016	A30017	A30018	A30019	A30020
Length in median line	(48)	—	(44)	44	43.5	—	—	48
Breadth across bases of cornua ..	—	(71)	—	—	(62)	(64)	(65)	—
Maximum breadth	—	(75)	—	—	—	—	—	—
Posterior breadth of inter-zonal part	(25)	26	(23)	22	(22)	26.6	—	—
Distance of pineal foramen from rostral end of shield	—	—	—	22.5	22.5	—	24.5	(26.5)
Distance of pineal foramen from posterior end of shield	—	23.5	22	21.4	20.5	—	—	(21)

The height of the shield could not be measured in any of the specimens but in no. 486 it is estimated at 7 mm at the posterior end of the inter-zonal part; the height is thus very small in proportion to the size of the shield. The variation in size is rather insignificant and on the whole the species attained only a medium size.

In general shape the cephalic shield is broad and very flat, the variations in shape are not great, some of the specimens are a trifle broader and more descreasing in breadth forwards than the others (cf. fig. 73 and Stensiö 1927, fig. 68). The maximum breadth of the shield, which lies across the middle parts of the cornua, is in some specimens somewhat more, in others somewhat less than one and a half times as great as the length of the shield in the median line, and equal to or somewhat less than the distance of the tip of the cornu from the rostral end of the shield. The rostral margin is broadly rounded without any rostral angle (the rostral angle present in the restoration of the shield, given by Stensiö 1927, fig. 68, is certainly attributable to the restoration of an imperfectly preserved specimen, cf. Stensiö 1927, pl. 37:1). The lateral margins are more or less strongly curved. The cornua, which project in posterior direction, are very long and slender, and slightly medially curved; they reach backwards far behind the posterior end of the inter-zonal part; their length constitutes about half of the distance of their tips from the rostral end of the shield. The inner margins of the cornua are devoid of denticles. The pectoral sinus are well defined and deep; their breadth is somewhat variable; in some

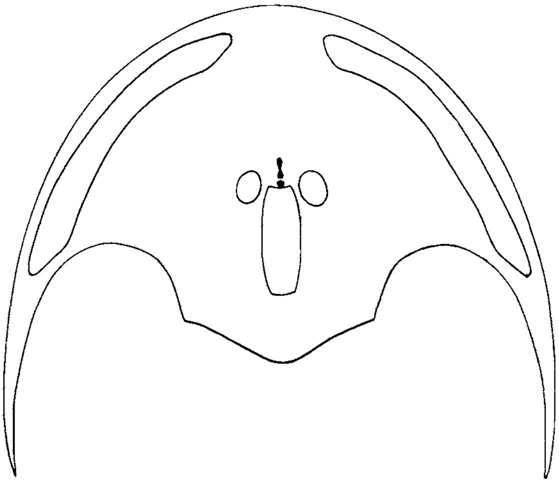


Fig. 73. — *Securiaspis staxrudi* (Stensiö). Restoration of the cephalic shield, dorsal view. After the specimens Pal. Mus. Oslo nos. A30016 —A30017 and ENS no. 486. Nat. size.

of the specimens there is a faintly pronounced antero-median corner. The inter-zonal part is rather long and narrow, narrowing gradually towards the postero-lateral angles; its breadth between these latter is contained not quite three times in the maximum breadth of the shield. The posterior margin forms medially a very obtuse angle which is protracted somewhat behind the postero-lateral angles; the margin between each of these angles and the posterior angle being almost straight or very sligtly concave. Dorsally the inter-zonal part is provided with a low but neatly defined sharp-edged median ridge. The dorsal sensory field is elongate, about two and a half times as long as broad, with slightly curved lateral margins, the anterior margin is truncated or slightly concave, the posterior margin more or less obtusely rounded. Posteriorly the field reaches well behind the openings of the ductus endolymphatici. The field is laterally bordered by a low obtuse ridge, which begins just postero-medially to the orbital openings and becomes more obsolete in passing backwards and disappears at the postero-lateral corners of the field. The distance of the posterior margin of the dorsal field from the posterior end of the shield is about two-thirds of the length of the field. The lateral sensory fields continue backwards on to the basal parts of the cornua and, as in the other species of the genus, lack any postero-median process extending medially unto the zonal part proper. The orbital openings are in general situated slightly nearer to the posterior than to the rostral end of the shield, and their distance from the pectoral sinus is much less than that from the posterior or rostral end of the shield; they are oval in shape. The circum-orbital ridge is apparently very feebly marked, but just in front of each orbital opening there is a strongly developed antorbital prominence. There is no independent pineal plate. The fossa circum-nasalis is semicircular in shape, and the naso-hypophyseal opening is situated on a small forwardly inclined ridge with only the foremost portion of the opening on the floor of the fossa.

The exoskeleton of the shield is imperfectly preserved. Its outer face is ornamented with very low, often hardly discernible, elongated, often much lengthened tubercles or ridges. Near the lateral borders of the shield and on the cornua, these ridges run parallely to the margins of the shield (as is noted by Stensiö 1927, p. 273). The superficial layer seems to be continuous and only subdivided by the circum-areal grooves. In the major part of the shield the middle layer contains well developed radiating vascular canals. Near the margins of the shield and on the cornua the radiating canals are replaced by canals disposed in rows running parallely to the margins of the shield and thus disposed conformably to the ornament of the outer face of the exoskeleton. In the inter-zonal part traces of ringsinus have been observed in the basal layer. The mucous canal system it only partly enclosed in the exoskeleton; it is developed as wide circum-areal grooves and as a fine-meshed network of rather fine intra-areal canals. The circum-areal grooves are often, especially in the anterior part of the shield, subdivided into rather narrow concentric grooves, anastomosing with each other by short transverse grooves; this subdivision of the circum-areal grooves is caused by the more or less lengthened tubercles or ridges placed in the grooves (pl. 65:2).

The endoskeleton is rather well ossified in several specimens. The canal sel_3 is undivided to about midway between the orbit and the lateral sensory field; in no. A30015 the conditions are somewhat different on the two sides, the canal on the right side dividing somewhat nearer to the lateral field than on the left side (but the differences between the two sides are not so strongly pronounced as in *S. kitchini,* Stensiö 1932, pl. 49:1). In nos. A30015 and A30020 an anterior branch of the canal V_3 is seen between the diverging branches of the canal sel_1. As regards the dorso-lateral superficial vein canals there are some peculiarities, noted above (p. 428) in the remarks to the genus; the conditions mentioned are met with in no. A30020.

Remarks. — With regard to the new material of this species now available and considering the rather insignificant rate of variation in the size and shape of the specimens it seems evident that we cannot retain the second specimen (no. 57), hesitatingly placed in this species by Stensiö (1927, pp. 272—274; fig. 69; pls. 34; 36:4), in the same species as the holotype but that is must represent a new species. There is, however, reason to believe that this specimen also will prove to be a *Securiaspis.* On account of the imperfect state of preservation and the distortion to which its shield has been subjected, it is not possible to obtain a correct idea of the real shape and proportions of the shield nor of several other important characters, e. g. the shape of the sensory fields. It is therefore preferable to await more and better preserved material before naming and diagnosing this species.

In the general shape of its cephalic shield *S. staxrudi* is most closely comparable to *S. kitchini* (Stensiö 1932, p. 160) and *S. quadrata*. It differs from both species by its comparatively great size and the very long and slender cornua, from *S. kitchini* furthermore by the posterior direction of the cornua, from *S. quadrata* by the shape of the inter-zonal part and the dorsal sensory field.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the upper parts: the horizon H (Stensiö 1927, p. 275), Mt Ben Nevis [W. of the First Glacier], in the horizon G.

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, W. Plateau, in the Benneviaspis horizon (nos. A30015—A30021); Mt Ben Nevis, without further indication as to locality (nos. 485—486). The specimen, no. A30022, hesitatingly placed here, was found on Mt Ben Nevis [W. of the First Glacier], in the horizon G.

The specimens nos. A30015—A30021 were collected in 1928 by Th. Vogt's expedition; nos. 485—486 by the ENS expedition in 1939.

2. *Securiaspis quadrata* n. sp.

(Fig. 74; pl. 64.)

Diagnosis. — A small *Securiaspis* species with maximum breadth of cephalic shield about one and a half times as great as length of shield in median line. Rostral margin obtusely rounded without any rostral angle; lateral margins convex. Cornua projecting in posterior direction, moderately long and slender, extending slightly behind posterior end of inter-zonal part. Length of cornua contained slightly more than three times in distance of their tips from rostral end of shield. Inner margins of cornua without denticles. Pectoral sinus fairly deep, with antero-median corner. Inter-zonal part comparatively short, broad, its breadth constituting somewhat less than half of maximum breadth of shield. Dorsal sensory field nearly three times as long as broad with maximum breadth in posterior half. Orbital openings large. Outer face of exoskeleton for the greatest part smooth; superficial layer continuous.

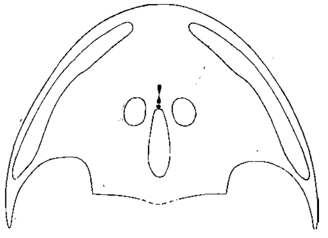
Holotype. — Cephalic shield (ENS no. 484).

Material. — The species is represented by the holotype (ENS no. 484) only, a cephalic shield in counter-part, wanting the posterior corner of the inter-zonal part and the distal half of the right cornu.

Description. — The dimensions of the cephalic shield are as follows: the length in the median line is about 26 mm, the maximum breadth is estimated at 42 mm, and the breadth of the inter-zonal part at the postero-lateral angles is 18 mm. The distance of the pineal foramen from the rostral end of the shield is 14 mm. The height of the shield could not be measured, but is obviously very small.

On the whole the cephalic shield is small, rather short, broad and flat with the maximum breadth (which lies near the tips of the cornua) about one and a half times as great as the length in the median line and distinctly greater than the distance of the tip of a cornu from the rostral end of the shield. The shield is fairly rapidly decreasing in breadth anteriorly. The rostral margin is uniformly rounded without any rostral angle. At the boundary between the rostral and the lateral margins there is on the right side a very obtuse and vaguely defined antero-lateral angle which is almost lacking on the left side, and there is a still more obtuse angle at the basis of the cornu. Probably the irregularities are peculiar to this single specimen and are not characteristic of the species. The lateral margins are fairly convex. The cornua are comparatively short and slender; their length constitutes slightly less than one-third of the distance of their tips from the rostral end of the shield; they are directed posteriorly and extend backwards to a point slightly behind the posterior end of the inter-zonal part; their outer margins are slightly curved in median direction, and their inner margins are devoid of denticles. The pectoral sinus are broad and fairly deep; they have a rather distinctly marked but rounded antero-median, and a much more obtuse antero-lateral corner. The inter-zonal part is comparatively short and broad with a rather uniform breadth decreasing very slightly towards the postero-lateral angles; the breadth is contained somewhat less than two and a half times in the maximum breadth of the shield. The posterior margin evidently forms a very obtuse median angle, which is very little protracted backwards. The margin between the posterior angle and each of the postero-lateral angles is almost straight. The dorsal sensory field is long and rather narrow; the length is almost three times as great as the maximum breadth, which lies at the posterior third of its length; the field is thus elongate, and reversely ovate in outline, the anterior and posterior margins being rather narrow. The distance of the posterior margin from the posterior end of the shield could not be measured but was evidently small. The lateral sensory fields extend backwards almost as far as to the middle of the length of the cornua. The orbital openings, which are very large in proportion to the size of the shield, are situated somewhat nearer to the posterior than to the rostral end of the shield; they are roundedly oval in shape. The antorbital prominence is quite inconsiderable. The circum-orbital ridge is very narrow and only slightly elevated on the lateral borders of the orbital openings. There is no independent pineal plate. The circum-nasal fossa is rather long and narrow, forming an acute-angled triangle.

Fig. 74. — *Securiaspis quadrata* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (ENS no. 484). Nat. size.



The exoskeleton is very imperfectly preserved. Apparently the superficial layer is continuous and smooth without any ornamentation except on the rostral and lateral margins of the shield, where the outer face is provided with low ridges, running parallelly to the margins as in *S. staxrudi.* In these places also the vascular canals are disposed in closely set rows in the same way as the superficial ridges. Elsewhere on the dorsal side of the shield there are regular radiating canals and the mucous canal system seems to form a fine-meshed network.

Only parts of the grooves of the sensory line system could be observed, which are indicated in fig. 74.

The endoskeleton is fairly well ossified and several of the superficial canals are exposed. The canal sel_1 reaches to a point about midway between the orbit and the lateral field, or somewhat nearer to the latter, before it bifurcates. The canal vls_3 opens into the canal *vcl* and with a small anterior part into the postero-dorso-lateral corner of the orbit; the canal vls_4 opens together with the canal vls_3 or slightly behind it into the canal *vcl.* The canals vls_5—vls_7 join apparently into a common trunk which opens into the canal *vcl.*

Remarks. — *S. quadrata* resembles *S. staxrudi* (p. 429 and Stensiö 1927, p. 272) and *S. kitchini* most closely, but differs from the first mentioned species mainly by the small size of the shield and by the comparatively short cornua, and from the latter, which is of about the same size, by a somewhat shorter shield, by the shape and direction of the cornua, and by the shape of the pectoral sinus, the inter-zonal part and the dorsal sensory field.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the upper parts (the Ben Nevis division).

Locality. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis. The single specimen was collected by the ENS expedition in 1939.

Securiaspis sp.

(Pl. 63:2.)

The specimen (Pal. Mus. Oslo no. A30023), described below, consists of a rather fragmentary cephalic shield, lacking parts of the rostral border and portions of the lateral regions including the two cornua; as it is also somewhat asymmetrically developed, it is impossible to restore the original shape of the shield. It is beyond doubt that we here have to deal with a form belonging to the genus *Securiaspis* but it can not with any certainty be referred to any of the known species of the genus, and possibly represents a species of its own.

Description. — The length of the shield in the median line amounts to about 31 mm and the breadth of the inter-zonal part across the postero-lateral angles is 15 mm; the distance of the pineal foramen from the posterior end of the shield is 14.5 mm. In size this specimen is comparable to *S. kitchini* and *S. quadrata*. The shield has with certainty been very broad. The rostral margin is broad and rounded but whether there was an obtuse rostral angle or not is impossible to say as the very apex of the rostral margin is lacking. The development and the direction of the cornua are unknown. The pectoral sinus are very probably broad and rather shallow; the preserved parts resemble those of *S. kingi*. The inter-zonal part is rather long and rapidly narrowing backwards; its seems very uncertain if a dorsal median crest was present. The dorsal sensory field is elongate and about two and a half times as long as broad with truncated anterior and posterior margins. The lateral sensory fields are not preserved. The orbital openings are roundedly oval in shape; they are situated somewhat nearer to the posterior than to the anterior end of the shield. There is no independent pineal plate. The short triangular fossa circum-nasalis is rather deep anteriorly. There is a distinct though rather low antorbital prominence as in *S. staxrudi*.

The superficial and middle layers of the exoskeleton are for the most part completely abraded but in some places we notice that the superficial layer is continuous and quite smooth, pierced by the pores of the mucous canal system, which system thus is enclosed in the exoskeleton and very probably forms a uniform, fine-meshed plexus. The horizontal vascular canals in the middle layer seem to have been developed as radiating canals and the corresponding canals along the lateral borders of the shield run in parallel rows along the margins.

Some parts of the endoskeletal canals are preserved. The canal sel_1 runs undivided to about midway between the orbit and the lateral field. The canal vls_3 opens directly into the orbit.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Ben Nevis division.

Locality. — Spitsbergen. E. side of Red Bay: in the moraine of the Andrée Glacier between Fraenkel Ridge and Mt Ben Nevis.

The single specimen was collected by the expedition of Th. Vogt in 1928.

Genus **Tegaspis** n. gen.

(τεγος, roof; πσἀις, shield.)

1927. *Cephalaspis* in part, Stensiö, pp. 246, 278—279.

Diagnosis. — A cephalaspid genus with rather broad cephalic shield. Cornua well developed, extending backwards at least as far as posterior end of inter-zonal part. Pectoral sinus broad, fairly well defined. Inter-zonal part rather short; dorsally with low median ridge; posterior angle very slightly protracted backwards; postero-lateral angles not protracted; posterior margin between posterior and postero-lateral angles not emarginate. Sensory fields well developed, consisting of an unpaired dorsal field and a pair of lateral fields; dorsal field rather short, lateral fields ending posteriorly in front of pectoral sinus, not extending backwards on to cornua, with strong postero-median process. No independent pineal plate. First nerve canal for lateral sensory field branching at a point about midway between orbit and lateral field. Canal for r. mandibularis trigemini running entirely behind first nerve canal for lateral sensory field. Common canal for united dorso-lateral superficial veins 3 and 4 opening behind orbit into canal for vena capitis lateralis. Superficial layer of exoskeleton discontinuous; middle layer with radiating canals; ringsinus well developed. Mucous canal system not enclosed in exoskeleton.

Type species. — *Cephalaspis kolleri* Stensiö.

Remarks. — This genus in erected for one species which differs from all other Cephalaspids in such a way that it is impossible to include it in any of the hitherto known genera without arbitrarily altering the definition of the respective genus.

With our present knowledge the genus *Tegaspis* is to be considered as probably akin to both *Benneviaspis* and *Cephalaspis*. It resembles the first genus in the disposition of the canal sel_1 and the canal vls_3 (this latter character is perhaps, as discussed before, p. 240, of minor importance), and to some extent as regards the shape of the lateral sensory fields. In both genera we observe a generally strongly developed postero-median process of the lateral field over the shoulder-girdle, but in *Benneviaspis* the lateral fields lie much nearer to the lateral margins of the shield and there is also a postero-lateral corner or process on to the basal part of the cornu; this process is entirely lacking in *Tegaspis* in which the lateral fields lie rather remote from the margins of the shield. *Tegaspis* differs furthermore from *Benneviaspis* with regard to the shape of the inter-zonal part and in the development of the exoskeleton: in *Tegaspis* the exoskeletal component of the inter-zonal part reaches much farther backwards than the endoskeletal component, and the margin between the posterior and the postero-lateral angles is not emarginate; in its middle layer the exoskeleton contains well developed radiating canals. *Tegaspis* also presents several characters in common with the genus *Ectinaspis* but differs from that genus by the dissimilar shape of the lateral sensory fields and the inter-zonal part, and also to some extent by the structure of the exoskeleton. From *Cephalaspis,* which genus *Tegaspis* resembles in the inter-zonal part and the minute structure of its exoskeleton, it differs by the disposition of the branches of the canal sel_1 and the canal vls_3, as well as by the shape of the lateral sensory fields. The species *C? pedata,* doubtfully referred to *Cephalaspis,* is in this latter respect intermediate between *Cephalaspis* and *Tegaspis.*

Tegaspis comprises as yet only the species *T. kolleri,* which (based on imperfectly preserved specimens) was originally referred to *Cephalaspis* by Stensiö (1927, p. 278).

The genus is only known from Spitsbergen, where it occurs in the upper division of the Red Bay series (Dittonian).

Tegaspis kolleri (Stensiö).

(Fig. 75; pls. 65:1; 66; 116:1.)

1927. *Cephalaspis kolleri,* Stensiö, p. 278; fig. 72; pls. 31:2; 32:3; 43:2 (not pl. 40:2).

Diagnosis. — Same as for genus (only species).

Holotype. — Cephalic shield (no. 60) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 278).

Material. — The material referable to this species consists of eight specimens (Pal. Mus. Oslo nos. A30010—A30013 and ENS nos. 480—483). No. 483 (pl. 66) consists of an almost complete cephalic shield, partly in counterpart; no. A30010 (pl. 65:1) of a fairly well preserved shield in counterpart, lacking most of its right side and the distal part of the right cornu, and no. 482 mainly of the dorsal exoskeleton of the right side of a shield, exposed in ventral view and showing some impressions of superficial nerve and vascular canals. The remaining specimens consist either (nos. 480—481) of rather incompletely preserved shields or (nos. A30011—A30013) only of fragments of such shields.

Description. — The length of the shield in the median line is estimated at 15 cm in no. 483 and at 13.5 cm in no. A30010. The breadth of the shield between the middle parts of the cornua is in no. 481 about 24 cm and in no. 483 21.5 cm. The posterior breadth of the inter-zonal part is in no. 483 7.4 cm and in no. A30010 7.2 cm, and its height is in no. 483 about 3.5 cm and in no. A30010 about 4 cm. All the shields seem to be of approximately the same dimensions and the species must have attained a very large size.

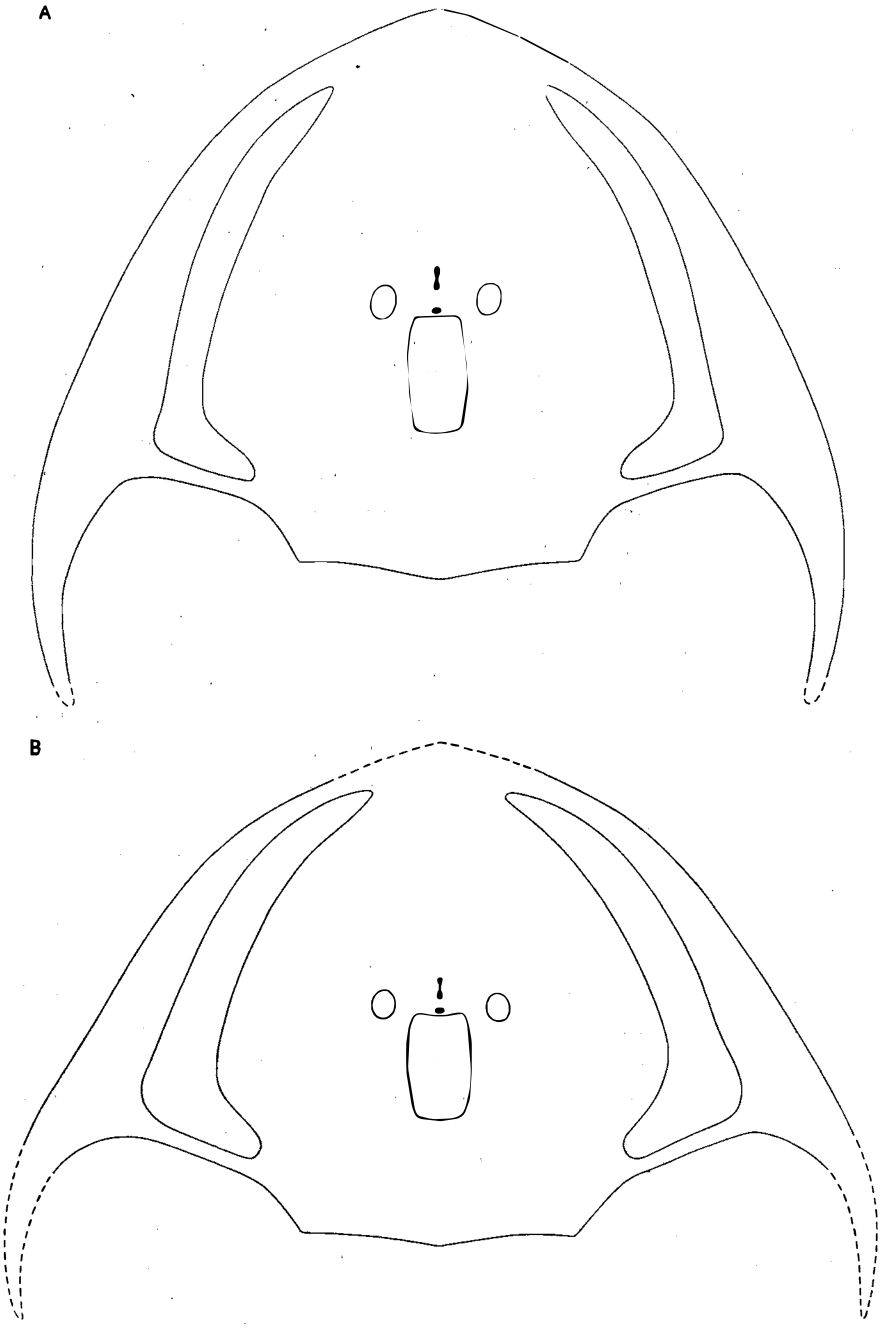


Fig. 75. — *Tegaspis kolleri* (Stensiö). Restoration of cephalic shields in dorsal view, A, after ENS no. 483, B, after Pal. Mus. Oslo no. A30010. ½.

The cephalic shield is somewhat variable in shape, being somewhat broader and shorter in some specimens than in others (see fig. 75A, B) but the maximum breadth of the shield is always considerable (about one and a half to one and three-quarter times) greater than the length of the shield in the median line. The maximum breadth is slightly or distinctly greater than the distance of the tip of a cornu from the rostral end of the shield. The shield narrows more or less rapidly forward. The lateral margins are somewhat more strongly curved at the bases of the cornua and at the transition into the rostral margin than in their middle parts; between the rostral and the lateral margin a fairly distinct but rounded and very obtuse antero-lateral angle is thus often developed. A more or less obtuse rostral angle is present. The cornua which are rather long, project in a posterior and slightly lateral or in a more postero-lateral direction and reach backwards behind the level of the posterior end of the inter-zonal part. The length of the cornua is contained probably about three times in the distance of their tips from the rostral end of the shield. The cornua are flattened in their basal half but more rounded in cross-section distally; they are distinctly curved in median direction and the maximum breadth of the shield does not lie between the tips of the cornua but across the middle parts. The "denticles", mentioned by Stensiö (1927, p. 278), are only a part of the general ornamentation of the outer face of the exoskeleton which occurs also on the median side of the cornua. The pectoral sinus are well defined, not very deep but rather broad although the breadth is somewhat variable; they have more or less distinctly defined antero-median and antero-lateral corners. The inter-zonal part of the shield is rather short and fairly narrow, decreasing in breadth towards its postero-lateral angles where the width is about one-third of the maximum breadth of the shield. The posterior angle of the inter-zonal part is very obtuse and reaches backwards to a point only slightly behind the postero-lateral angles. The posterior margin between the posterior and the postero-lateral angles is almost straight when viewed from above. Dorsally the inter-zonal part is provided with a low, broad, not very sharp-edged ridge which extends from a point just behind the dorsal sensory field on to the posterior end of the shield. The dorsal sensory field is slightly variable in shape, being rather short and broad or fairly narrow, and about one and a half times to about twice as long as broad; its lateral margins are almost straight and the anterior and posterior margins are on the whole truncated, the anterior one is often somewhat emarginate; the field is thus almost rectangular in outline. The distance between the posterior margin of the field and the posterior end of the shield is somewhat greater than the length of the field. The lateral sensory fields gradually taper anteriorly towards their rather pointed anterior ends. They lie here fairly near to the antero-lateral margins of the shield but on running backwards diverge from the lateral margins of the shield and are directed towards the zonal part in front of the pectoral sinus; they are here provided with a rather strongly developed postero-median process which extends towards the inter-zonal part but which does not enter this part. Thus the fields do not extend on to the cornua, and they have antero-medially to the bases of the cornua no lateral process but an almost right-angled and strongly rounded postero-lateral corner. The distance between the antero-median ends of the two fields is variable, being one and a half to two and a half times as great as the inter-orbital breadth. The orbital openings, which are roundedly oval in shape, are very small in proportion to the size of the shield; they are situated at about the middle of the length of the shield in the median line. The circum-orbital ridge is strongly developed. The antorbital prominence is pronounced. The pineal foramen is not located in a separate plate. The naso-hypophyseal opening is small and narrow. The circum-nasal fossa is broad and shallow, not very well defined.

The exoskeleton (cf. pl. 116:1) is rather imperfectly preserved. Its outer face is ornamented with tubercles. In front of the naso-hypophyseal opening in no. 481 there are large but probably rather flattened tubercles, each of them situated in the centre of a polygonal area and surrounded by rather numerous small, more or less elongated tubercles; laterally to the posterior part of the lateral sensory field in the same specimen there are, however, only small tubercles, closely set, but irregularly disposed. The superficial layer and the outer division of the middle layer are present only in the tubercles. The lower division of the middle layer contains radiating canals of very fine calibres. The basal layer contains rather wide ringsinus which divide the layer into distinct polygonal areas. These polygonal areas are of very varying size in the different parts of the shield; in the inter-zonal part in no. 483 they are on the average 4 mm in diameter but laterally to the posterior part of the lateral sensory field in the same specimen there are polygonal areas measuring only about 2 mm in diameter. The mucous canal system was not enclosed in the exoskeleton but was situated in open circum-areal grooves; whether there also are intra-areal grooves or not, could not be ascertained. The ornamentation of the plates covering the sensory fields consists of small tubercles.

The endoskeleton is imperfectly or not at all preserved. In some specimens (nos. 482—483) the canals for superficial nerves and vessels could be seen. The canal sel_1 is divided into two branches at a point about midway between the orbit and the lateral field. The canals vls_3 and vls_4 unite to form a short common trunk which opens into the canal *vcl* behind the orbit; the canal vls_5 and vls_6 apparently also join into a common canal before opening into the canal *vcl*.

Remarks. — The species *T. kolleri* originally was included in the genus *Cephalaspis* (Stensiö 1927, p. 278). As seen from the description of the better preserved material now at hand, it is evident that the species cannot pertain to this genus but must form a genus of its own.

In the general shape of its shield the species is much *Cephalaspis*-like, and fragmentary shields not showing the characteristic generic features, can possibly be confused with some of the larger species in this genus, e. g. *C. tenuicornis* (in which the cornua are rather similar to those in *T. kolleri)* and *C? pedata.* If parts of the lateral sensory field are preserved, exhibiting either the pointed anterior end or the peculiar shape of the posterior part, the shields or shield-fragments of *T. kolleri* are easily recognizable.

Of the original material of *C. kolleri,* no. 61 (Stensiö 1927, pl. 40:3) and no. 63 do not belong to this species.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Ben Nevis division.

Localities. — Spitsbergen. E. side of Red Bay: the Andrée Glacier, S. half, W. part, in the moraine (nos. 481, 483); Mt Ben Nevis, in talus (nos. 480, 482), in the horizon f—g (no. A30012), in the Benneviaspis horizon (no. A30011), S. E. slope, in the talus masses (“Ben Nevis Uren SØ Skr.”; no. A30013), the Second Glacier, in the moraine (“Cephalaspis moraine”; no. A30010).

The specimens nos. A30010—A30013 were collected by Th. Vogt’s expedition in 1928, the others (nos. 480—483) by the ENS expedition in 1939.

Genus **Ectinaspis** n. gen.

(εκτεινειν, to spread out; ἀσπις, shield.)

Diagnosis. — A cephalaspid genus with broad and depressed cephalic shield. Cornua well developed, directed postero-laterally and extending backwards behind posterior margin of inter-zonal part. Pectoral sinus well developed but shallow. Inter-zonal part broad and rather long without dorsal ridge or spine; posterior angle rounded, postero-lateral angles slightly protracted. Sensory fields well developed, consisting of an unpaired dorsal and one pair of lateral fields; dorsal field broad and short, lateral fields extending only over basal parts of cornua, with distinct postero-medially protracted angle. Orbital openings situated about midway on shield. Independent pineal plate present. First nerve canal for lateral sensory field running undivided until somewhat medially to lateral field. Canal for dorso-lateral superficial vein 3 opening into postero-lateral corner of orbit. Superficial layer of exoskeleton (probably) continuous, middle layer with radiating canals. Mucous canal system enclosed in exoskeleton.

Type species. — *Ectinaspis heintzi* n. sp.

Remarks. — This genus is only a provisional one, based as it is only on one species, which furthermore is represented by a single, partly imperfectly preserved specimen. In its structure it is connected to some other well defined genera, but it cannot be included in any of them. Temporarily it seems to be most advisable to classify this aberrant species in a genus of its own.

The genus *Ectinaspis* can be compared most closely with *Cephalaspis, Benneviaspis, Tegaspis* and *Securiaspis.* In the general shape of the cephalic shield, *Ectinaspis* resembles some species of *Cephalaspis* (e. g. *C. woodwardi* and *C. deltoides)* but the differences are striking if attention is paid to the disposition of the canal sel_1, the short dorsal sensory field, and the postero-median angles of the lateral sensory fields (this angle is, however, indicated in some *Cephalaspis* species, viz. *C. salweyi, C. metopias* and *C? pedata).* The canal vls_3 opens into the orbit as in *Cephalaspis* but (as mentioned before, p. 240) this character is probably of minor importance. With regard to the disposition of the canal sel_1 this new genus reminds of *Benneviaspis, Securiaspis* and *Tegaspis,* in particular the first one, in which the canal branches rather far antero-laterally. From *Tegaspis,* which it resembles in the shape of the dorsal sensory field, *Ectinaspis* differs by the development of the lateral sensory fields, the presence of a pineal plate, and by the general shape of the shield. In this latter respect it reminds, to a certain degree, of some species of *Benneviaspis* and *Securiaspis.* It differs from *Benneviaspis* by the development of the inter-zonal part and by the structure of the exoskeleton; from *Securiaspis* it differs by the short inter-zonal part, by the shape of the lateral sensory field and by the short dorsal field, and from both genera by the possession of a pineal plate.

It seems as if *Ectinaspis* is possibly more closely related to *Benneviaspis* or *Tegaspis* than to *Cephalaspis* and *Securiaspis,* and this supposition is based mainly upon the development of the canal sel_1 and the shape of the lateral sensory field.

The genus *Ectinaspis* contains as yet only the type species, *E. heintzi.*

Ectinaspis is only found in Spitsbergen and here in the lower divison of the Red Bay series (Dittonian).

Ectinaspis heintzi n. sp.
(Fig. 76; pl. 67.)

Diagnosis. — Same as for genus (only species).

Holotype. — Cephalic shield (no. A30014) in the Palaeontological Museum, Oslo.

Material. — The species is represented only by the holotype (Pal. Mus. Oslo no. A30014), which consists of a fairly complete cephalic shield in counterpart, lacking a postero-lateral portion of its right side.

Description. — The length of the shield in the median line is 31 mm, the maximum breadth, which lay between the tips of the cornua, is estimated at 65 mm, the distance from the tip of the cornu to the rostral end of the shield is 47 mm, and the maximum height, at the posterior end of the inter-zonal part, can be estimated at 7—8 mm. The breadth of the inter-zonal part across the postero-lateral angles is about 22 mm. The distance of the pineal groove from the rostral end of the shield is 14.8 mm, and from the posterior end 15.5 mm. As seen from the measurements the cephalic shield is rather small and on a whole very broad and flat.

The maximum breadth of the shield is about twice as great as the length of the shield in the median line and about one and a third times as great as the distance of the tip of a cornu from the rostral end of the shield. The shield very rapidly narrows forward. The rostral margin is evenly curved without any trace of a rostral angle, and there are no antero-lateral angles between the rostral and lateral margins. The lateral margins form an almost straight line from the rostral margin as far backwards as to the middle of the length of the cornua. The cornua are directed postero-laterally; in their distal parts they are slightly bent in posterior direction; they are long and fairly strongly built and taper very slightly towards their tips which are bluntly rounded; the length of the cornua is contained about two and a half times in the distance of their tips from the rostral end of the shield. The median margins of the cornua are not provided with any real denticles; there are, however, both on the median and the lateral margins (and probably all over the cornua) small blunt tubercles. The pectoral sinus are very broad and shallow, without any antero-lateral or antero-median corners. The inter-zonal part is short and very broad and somewhat narrowing backwards, its breadth between the postero-lateral angles constituting just about one-third of the maximum breadth of the shield; the postero-lateral angles are somewhat protracted backwards, and the posterior margin between them and the posterior angle is slightly emarginate but not nearly as distinctly as in e. g. *Benneviaspis.* The posterior end of the inter-zonal part is rounded, not forming any distinct posterior angle, and reaches backwards about as far as the pestero-lateral angles. Most likely there is no dorsal crest or spine. The dorsal sensory field is fairly short and broad, about twice as long as broad. The rather narrow transverse anterior margin lies immediately behind the pineal groove; the lateral margins are fairly distinctly convex, and the posterior margin is abruptly truncated. The ductus endolymphatici opened in the postero-lateral corners of the dorsal field. The distance of the posterior margin of the field from the posterior end of the shield is about one and a half times as great as the length of the field. The lateral sensory fields are rather narrow with somewhat varying breadth, and narrowest between the branches of the canals for

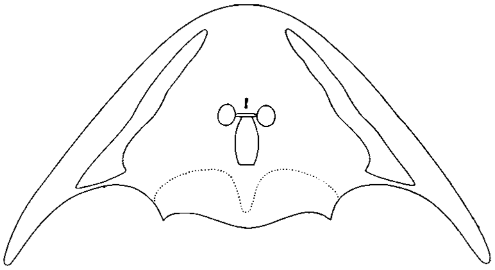


Fig. 76. — *Ectinaspis heintzi* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (Pal. Mus. Oslo no. A30014). The posterior margin of the endoskeleton indicated by dotted line. Nat. size.

the third and fourth nerves to the field; posteriorly to this section they widen, reach postero-laterally on to the basal part of the cornua, and are postero-medially provided with a distinct angle or short process on the zonal part in front of the pectoral sinus. The distance between the antero-median ends of the two lateral fields is between three and four times as great as the inter-orbital breadth. The orbital openings, which are almost circular in shape, are situated at about the same distance from the rostral as from the posterior end of the shield and from the pectoral sinus; they are surrounded by a thin but rather high circum-orbital ridge. The inter-orbital breadth is rather small, being slightly greater than the transverse diameter of an orbital opening. No antorbital prominence seems to have been developed. A pineal plate was developed (not preserved). The anterior portion of the naso-hypophyseal opening is situated on the floor of a rather broad fossa circum-nasalis, while the middle and the posterior portion lie on a small, posteriorly more elevated, ridge.

The exoskeleton is well developed but its outer parts are not easily accessible to examination. The superficial layer was probably continuous and smooth without ornamentation, at least this seems to be the case along the anterior margins of the shield. On the cornua, both on their median and lateral margins, as well as along the posterior margin of the zonal part at the inner end of the pectoral sinus a few small, blunt tubercles are, however, observed. In the middle layer, there are distinct bundles of radiating canals of comparatively fine calibre. The radiating canals form rather distinct vascular areas with an average diameter of 1.4 mm. In the most postero-lateral portion of the inter-zonal part there are on the ventral face of the exoskeleton some grooves (encircling polygonal areas), which probably correspond to the ring-sinus in other Cephalaspids. The basal layer of the exoskeleton is comparatively thick. The mucous canal system is very probably entirely enclosed in the exoskeleton and, as far as could be ascertained, consists of a uniformly fine-meshed plexus.

The endoskeleton is rather imperfectly preserved and the canals are difficult to observe. The endoskeletal component in the inter-zonal part is rather strongly emarginate between its posterior and postero-lateral ends and terminates much farther anteriorly than the exoskeletal component. The canal sel_1 divides in two separate branches just medially to the lateral sensory field. The canal vls_3 opens directly into the postero-dorso-lateral part of the orbit; the canals vls_4 and vls_5 apparently unite into a common trunk before opening into the canal *vcl,* whereas the canal vls_6 runs directly to this canal.

Remarks. — *Ectinaspis heintzi* is named in honour of Professor Anatol Heintz of the University of Oslo, the eminent expert on fossil fishes, who has participated in many expeditions to Spitsbergen; he was i. a. one of the leaders of the ENS expedition in 1939, and has collected a large part of the material here described.

The species is distinguished by the characters given in the generic diagnosis, and the specimens belonging to it can, when adequately preserved, easily be determinated. In the general shape of its shield the species resembles some Spitsbergen *Cephalaspis* species, *C. deltoides* and *C. divaricata,* and also slightly the much smaller *Benneviaspis longicornis.*

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Primaeva horizon.

Locality. — Spitsbergen. E. side of Red Bay: Fraenkel Ridge, S. W. part, in the Primaeva horizon.

The single specimen was collected by Th. Vogt's expedition in 1928.

Genus **Benneviaspis** Stensiö.

1927. *Benneviaspis,* Stensiö, p. 288.
1932. *Benneviaspis,* Stensiö, p. 152.

Diagnosis. — A cephalaspid genus with short, broad and depressed cephalic shield. Anterior margin of shield obtusely rounded without rostral process. Cornua fairly well to strongly developed, projecting in postero-lateral direction but never extending far behind posterior end of inter-zonal part. Pectoral sinus broad and usually shallow. Inter-zonal part closed ventrally, rather rapidly narrowing backwards, with protracted posterior and postero-lateral angles and distinct inter-zonal sinus; dorsally without median ridge or spine. Sensory fields well developed, consisting of an unpaired dorsal field and one pair of lateral fields; lateral fields extending over proximal parts of cornua; provided with more or less marked postero-median angle or with strongly developed postero-median process on to inter-zonal part in front of postero-lateral angles. No pineal plate. First nerve canal for lateral sensory field extending undivided at least as far as midway between orbit and lateral field. Main part of canal for r. mandibularis trigemini lying behind first nerve canal for lateral sensory field. Canal for dorso-lateral superficial vein 3 generally opening into canal for vena capitis lateralis behind orbit. Superficial layer of exoskeleton continuous. No radiating canals in middle layer. Mucous canals system enclosed in exoskeleton, forming fine-meshed plexus. (Modified after Stensiö 1932.)

Type species. — *Benneviaspis holtedahli* Stensiö (1927, by monotypy).

Remarks. — To the characters of the genus given in the diagnosis above the following comments and supplements may be added.

The canal sel_1 divides in general into two separate branches distinctly nearer to the lateral field than to the orbit; an exception from this rule presents the *Benneviaspis* sp. figured by Stensiö 1932 (pl. 48:1). The canal vls_3 or the common trunk arising from the junction of the canals vls_3 and vls_4 generally opens into the canal *vcl* behind the orbit but sometimes in the postero-dorso-lateral part of the orbit; this character has evidently not been firmly established in the genus. The canal *vcl* runs behind the orbit in a straightly posterior direction. The inter-zonal sinus are distinct and the exoskeletal component extends backwards slightly behind the endoskeleton. With regard to the shape of the lateral sensory fields the species of the genus can be split into two groups. In the first group, which comprises *B. holtedahli, B. lankesteri, B. anglica, B. longicornis, B. platessa,* and *B.* sp. 1, the postero-median angle of the fields is only indistinctly protracted *(B. longicornis)* or forms a moderately developed process over the zonal part in front of the pectoral sinus. The second group includes *B. grandis* and *B. lövgreeni,* and here the postero-median process is very strongly developed, extends backwards to the inter-zonal part of the shield and ends in front of the postero-lateral angles; in this respect the fields remind of those in *Boreaspis.*

As to the systematic postition of *Benneviaspis,* Stensiö (1927, p. 288; 1932, pp. 152, 153) has emphasized that the genus is most closely akin to *Hoelaspis, Boreaspis, Kiaeraspis,* and *Securiaspis* and on the same argumentation as used by him the new genera *Tegaspis, Ectinaspis, Nectaspis,* and *Axinaspis* can also be taken into consideration. The genus must, however, be considered as most closely related to the genera *Hoelaspis* and *Boreaspis* on account of resemblances in the general shape of the cephalic shield, a similar development of the inter-zonal part, of likenesses in the shape of the sensory fields as well as with regard to the similar minute structure of the exoskeleton.

It seems not at all improbable that the ancestors of *Hoelaspis* are to be searched for in some species group in *Benneviaspis,* possibly closely related to *B. longicornis.*

The following named species are at present included in the genus, viz. *B. lankesteri* Stensiö and *B. anglica* Stensiö from the Dittonian of England, *B. holtedahli* Stensiö, *B. longicornis* Wängsjö and *B. platessa* n. sp. from the Red Bay series in Spitsbergen, *B. grandis* n. sp., *B. maxima* n. sp. and *B. lövgreeni* n. sp. from the Wood Bay series in Spitsbergen. It can be added that the genus is also represented in the Old Red of Podolia (according to verbal information by W. Zych and later confirmed by some specimens which I have seen).

It may be noted here, that a fragment of a large cephalaspid shield from the Wood Bay series, described and figured by Stensiö 1927 (p. 285; pl. 6:2), with all probability belongs to the genus *Benneviaspis* (see below, p. 465). An imperfect cephalic shield, hesitatingly placed in *Cephalaspis arcticus* by Stensiö (1927, p. 280; pl. 40:5), also belongs to *Benneviaspis;* the shield reminds of that of *B. holtedahli* but is much smaller, and probably represents a new species.

With regard to its geological range the genus was so far known to occur in the Dittonian of England, and in Spitsbergen in the Red Bay series, in age corresponding to the Dittonian, but is now also found with three species in the lower division of the Wood Bay series (which very probably is of Siegenian age), and with one *(Benneviaspis* sp. 2) in the upper parts of the same series.

A. Species from the Red Bay series.

1. *Benneviaspis longicornis* Wängsjö.

(Fig. 77; pl. 68:3.)

1937. *Benneviaspis longicornis,* Wängsjö, p. 209; figs. 1—2.

Diagnosis. — A *Benneviaspis* species of small size with maximum breadth of cephalic shield probably more than twice as great as length of shield in median line. Lateral margins of shield distinctly concave. Cornua directed laterally and slightly backwards, slender and very long; inner margins without denticles. Pectoral sinus very shallow. Inter-zonal part rapidly narrowing backwards, its posterior breadth less than one-third of maximum breadth of shield; posterior angle reaching backwards beyond tips of postero-lateral angles. Dorsal sensory field about three times as long as broad. Lateral sensory fields extending backwards on basal part of cornua, with obtuse postero-median angle on shoulder-girdle.

Holotype. — Cephalic shield (no. A24900) in the Palaeontological Museum, Oslo.

Description. — For a detailed account, the reader is referred to the original description. Here only some corrections and addenda will be given, as well as a new restoration of the cephalic shield (fig. 77). In the original restoration the lateral and the rostral margins were thought to be evenly curved but considering the shape of the shield in some other *Benneviaspis* species *(B. lankesteri, B. anglica, B. grandis,* some specimens of *B. holtedahli* and especially an undetermined species

Fig. 77. — *Benneviaspis longicornis* Wängsjö. New restoration of the cephalic shield, dorsal view. After the holotype (Pal. Mus. Oslo no. A24900). Nat. size.

from Podolia) and in *Hoelaspis,* I now think it not improbable that an obtuse antero-lateral angle was present between the lateral and the rostral margins. The configuration of the rostral margin is unknown and there is nothing to prove that it was shaped as in the new restoration but the fact that *B. longicornis* is very similar in other respects to an undescribed species from Podolia, in which the rostral margin is very obtusely rounded. The most distal portion of the cornua is very slightly inclined backwards, a character which is also met with in *B. grandis* and in *Hoelaspis.* The breadth of the inter-zonal part between the postero-lateral angles is rather small, constituting not quite one-third of the maximum breadth of the shield. The dorsal sensory field is elongate and somewhat reversely ovate in shape, the maximum breadth lying a little behind the middle of the length of the field. The field tapers anteriorly to a point closely behind the pineal foramen. The lateral fields have no postero-medial process over the zonal part of the shield but are somewhat widened posteriorly and provided with an obtuse postero-median angle. Further cleaning of the specimen has made it almost certain that there is no independent pineal plate. The naso-hypophyseal opening is rather large in proportion to the size of the shield and in comparison to other species of the genus; it is very clearly subdivided into three sections and has not the narrow shape which is characteristic for the other species of the genus.

With regard to the endoskeletal canals it must be noted that the proximal courses of the dorso-lateral superficial veins are often followed with difficulty as the canals are widened and connected with each other so as to form a sinus plexus. The canal vls_3 opens on the left side into the postero-dorso-lateral corner of the orbit; on the right side it apparently opens into the canal *vcl* behind the orbit.

Remarks. — Previously (Wängsjö 1937, p. 211) I have pointed out the resemblances which exist between this species and the genera *Securiaspis* and *Hoelaspis.* More particularly it shows a certain likeness to *Securiaspis kingi* (Stensiö 1932, p. 162; the placing of the species in this genus is, however, open to some doubt) but it differs from this species and from the genus *Securiaspis* in general mainly by the development of the inter-zonal part of the shield. The similarities of the species with the genus *Hoelaspis* are especially significant as the genera *Benneviaspis* and *Hoelaspis* are thought to be very closely akin. One of the most striking differences between them lies in the absence or presence of a rostral process. As the single specimen known of the species *B. longicornis* is imperfectly preserved with regard to the anterior part of its shield nothing definite can be said about the shape of its rostral margin; if the species really was provided with a rostral process it cannot be maintained in the genus *Benneviaspis* but must probably be transferred to the genus *Hoelaspis*. But, as said above, *B. longicornis* is very similar in the general shape of its shield to an undescribed Podolian species which undoubtly belongs to *Benneviaspis,* and I am therefore pretty certain that *B. longicornis* really belongs to the same genus. To the other species from Spitsbergen and England it shows no closer affinities and is easily distinguished from them by the small size of its shield, and the slender and almost straight cornua.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series (Ben Nevis division), the Vogti horizon.

Locality. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, North Plateau, 600 m.

The single specimen was collected by Th. Vogt's expedition in 1928.

2. *Benneviaspis holtedahli* Stensiö.

(Fig. 78; pls. 69—71.)

1927. *Benneviaspis holtedahli,* Stensiö, p. 289; fig. 76; pls. 41—42; 43:1.

Diagnosis. — A *Benneviaspis* species of medium size with maximum breadth of cephalic shield about twice as great as length of cephalic shield in median line. Rostral margin more or less rounded, without rostral angle. Lateral margins of shield almost straight to rather convex. Cornua broad and fairly long, their length constituting about one third of distance from their tips to middle of rostral margin. Inner margin of cornua without denticles. Pectoral sinus very broad and shallow. Inter-zonal part rapidly narrowing backwards, its posterior width contained about three times in maximum breadth. Dorsal sensory field of varying form, rather broad, with narrow posterior projection behind openings for ductus endolymphatici. Lateral sensory field with rather long postero-median projection over zonal part. Orbital openings situated somewhat nearer to posterior than to rostral end of shield.

Holotype. — Cephalic shield (no. 70) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 289).

Material. — In the new material at my disposal, the species in question is represented by no less than fourteen specimens, viz. Pal. Mus. Oslo nos. A24381, A30001—30009, ENS nos. 477—479, 613, of which six, nos. A30001 (pl. 70:2), A30002 (pl. 71:3), A30004 (pl. 71:2), A30008, 477, 478, consist of rather completely preserved cephalic shields in counterpart and five, nos. A30003 (pl. 69), A30005 (pl. 70:1), A30006 (pl. 71:1), A30007, A24381 of fairly well preserved shields,

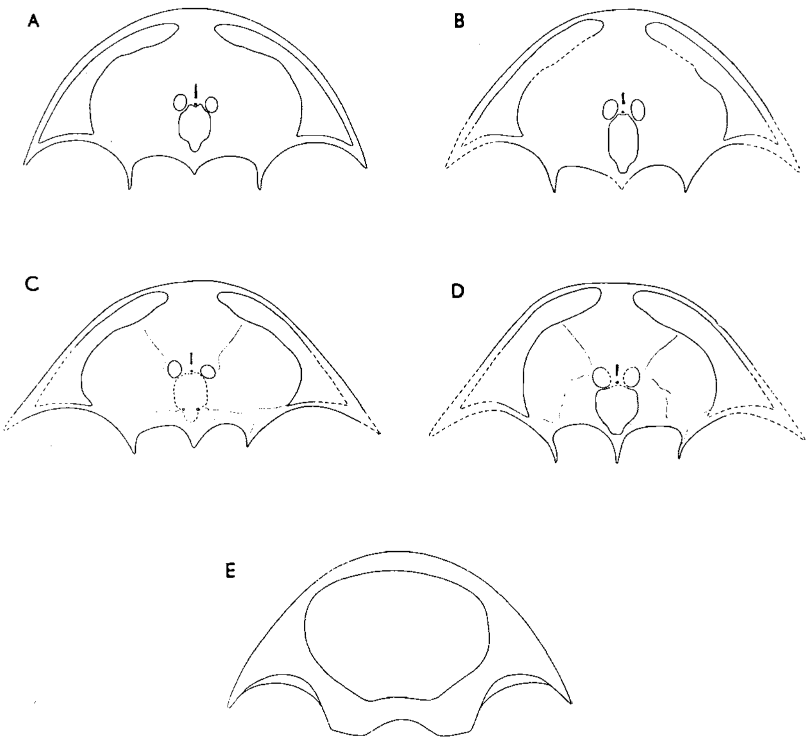


Fig. 78. — *Benneviaspis holtedahli* Stensiö. Restorations of cephalic shields, A—D in dorsal, E in ventral view; A, after ENS no. 478, B, after Pal. Mus Oslo no. A30008, C, after Pal. Mus. Oslo no. A30001, D, after Pal. Mus. Oslo no. A30003, E, mainly after Pal. Mus. Oslo no. A30006. ¾.

while the remaining three, nos. A30009, 479, 613, consist of fragmentary shields only. In addition to these specimens I place here with some hesitation two rather small shield fragments (nos. 614, A30100), too imperfectly preserved as to be definitely determined.

Description. — The dimensions (in mm) of some of the cephalic shields are given below (a figure in brackets indicates an estimated measure).

Nos.	477	478	A24381	A30001	A30002	A30003	A30004	A30005	A30008
Length in median line	29	29	(32)	29	33	31	—	(35)	(31)
Maximum breadth ..	62	61	66	(65)	70	—	(73)	—	(63)
Breadth of inter-zonal part, posteriorly ..	22	22.5	(24)	20	23	23	—	22	23
Distance of pineal foramen from rostral end of shield ..	(16)	(15)	18	16	19	18.5	19	19	18
Distance of tip of cornu from rostral end of shield	42	41	45	41	46	—	(45)	—	(42)

The real height of the shield could be measured only in one specimen, viz. no. A30003, where it amounts to 8 mm at the posterior end of the inter-zonal part. As is seen from the measurements given above and also from the restorations of some of the cephalic shields (fig. 78A—E) the shield of this species is of rather variable size and shape. On the whole the shield is very broad and flat; its maximum breadth, which lies between the posterior ends of the cornua, is about (or most often somewhat more than) twice as great as the length in the median line and about one and a half times as great as the distance of the tip of a cornu from the rostral end of the shield.

In the following are noted some variations in the characters of the cephalic shield and some divergences from the original description as also some addenda to it; for the rest the reader is referred to the exhaustive description by Stensiö (1927, pp. 289—291).

The rostral margin of the shield is generally uniformly rounded, but exceptions occur in some specimens; it is thus very obtuse in no. A30003, and in no. A30002 there is a faint indication of a rostral angle; both these specimens exhibit a very obtuse but rather distinct angle at the transition of the rostral to the lateral margins as is the case in the British species *B. lankesteri* and *B. anglica.* The lateral margin is generally convex but in some specimens (nos. A30001, A30006, A30007) it is rather straight and this fact is partly connected with the shape and direction of the cornua. These latter are mostly of a short triangular shape (cf. Stensiö 1927, fig, 76A) but the length is somewhat varying, and in some specimens the cornua can project in a more or less posterior direction; they reach, however, never behind the posterior end of the shield. According to the direction of the cornua, the pectoral sinus are of a variable shape. In no. A30006 it is distinctly seen that the zonal part reaches farther backwards dorsally than ventrally or, in other words, that the transverse posterior wall of the shoulder-girdle is inclined in a dorso-posterior to ventro-anterior direction and that the pectoral sinus thus has a different shape in dorsal and in ventral view, being shallower in the first case than in the second. The inter-zonal sinus are of varying depth but they are deep or rather deep, and never shallow. The postero-lateral angles reach backwards to about the same level as the posterior angle; in some cases they are very narrow and form in reality only the upper margins of the lateral walls of the inter-zonal part. The posterior margin of the ventral portion of the inter-zonal part is medially somewhat emarginate, much as in *B. grandis.* The shape of the sensory fields varies to some extent; the lateral fields are generally much broader than in the restoration given by Stensiö (1927, fig. 76A), and their postero-median process is considerably better developed, more in conformity with those of *B. lankesteri* and *B. anglica* (cf. Stensiö 1932, figs. 55—56). The dorsal field is of varying breadth and length but generally rather characteristically shaped; in the posterior third of its length, on a level with the openings for the ductus endolymphatici, it narrows, often abruptly, in such a way that a median process is formed posterior to the main field. In an analogous way the field is often, especially when its breadth is very great, narrowed anteriorly between the posterior parts of the orbits. In nos. 614 and A30003 the dorsal field is very strongly developed, reminding of the field in the *Benneviaspis* species from the Wood Bay series. No independent pineal plate is present. The naso-hypophyseal opening is lengthened and narrow, with the three divisions indistinctly differentiated. The circum-nasal fossa is rather shallow and narrow, forming a very acutely angled triangle.

The exoskeleton is very imperfectly preserved in most of the specimens. The superficial layer is continuous and generally quite smooth, only along the rostral and lateral margins there is an ornamentation of very delicate, low ridges, running parallelly to the margins. The mucous canal system was very probably developed as a fine-meshed network without any differentiation in circum-areal and intra-areal canals. No radiating vascular canals in the middle layer have been observed in any of the specimens. There are no ringsinus in the basal layer.

Some of the grooves of the sensory line system have been observed in several specimens, it suffices to notice that a posterior part of the main lateral line is found on the postero-lateral angles of the inter-zonal part.

Several of the internal structures are seen in the different specimens. The canal vls_3 is not distinctly seen in the specimens figured by Stensiö (1927, pls. 41—42; 43:1); in no. A30005 of the new material the canal in question must have opened into the canal *vcl* just behind the orbit; in nos. A30001 and A30004 it joins the canal vcl_4 (as is the case in *B. lankesteri, B. anglica,* and *B.* sp., Stensiö 1932, figs. 10—12; pls. 47:2; 48) and the common trunk, thus formed, opened very probably into the postero-dorso-lateral corner of the orbit (and not directly into the canal *vcl* behind the orbit as in the British species just mentioned).

Remarks. — *B. holtedahli* resembles rather much *B. lankesteri* (Stensiö 1932, p. 153) but is distinguished from this species by the somewhat differently shaped cornua and principally by the shape of the dorsal sensory field. Among the Spitsbergen species it reminds in size and shape much of the unnamed species 2 (p. 466) from the Wood Bay series but its shield is broader, the cornua shorter, and the orbits placed rather far backwards on the shield.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the Ctenaspis and Benneviaspis horizons.

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, in talus (nos. 477—479, 613), plateau 350 m (no. A24381), [W. plateau, 300—400 m], in the Ctenaspis horizon (nos. A30001, A30003), [W. side, 500—600 m], in the Benneviaspis horizon (nos.

A30002, A30004—A30009). — Localities of the two specimens, hesitatingly placed here: Mt Ben Nevis, in the Benneviaspis horizon (no. A30100); S. of the Andrée Glacier, fossiliferous horizon about 50 m above sea-level (no. 614).

The specimen no. A24381 was collected by Th. Vogt's expedition in 1925, nos. A30001—A30009, A30100 by his expedition in 1928, and nos. 477—479, 613—614 by the ENS expedition in 1939.

3. *Benneviaspis platessa* n. sp.

(Fig. 79; pl. 72:2.)

Diagnosis. — A large *Benneviaspis* species with maximum breadth of cephalic shield somewhat more than twice as great as length of shield in median line. Rostral margin convex, (probably) without angles at transition to lateral margins. Cornua long and slender, projecting in postero-lateral direction; inner margins without denticles. Pectoral sinus very broad and fairly shallow. Dorsal sensory field elongately oval, about twice as long as broad. Lateral sensory fields broad with triangular postero-median process over zonal part in front of pectoral sinus. Orbital openings very small in proportion to size of shield, lying probably far behind middle of length of shield in median line.

Holotype. — Fragmentary cephalic shield (no. A24901) in the Palaeontological Museum, Oslo.

Material. — In this species I place with certainty only the holotype (Pal. Mus. Oslo no. A24901); it consists mainly of the dorsal exoskeleton of a cephalic shield, exposed in ventral view; the shield is very imperfect, lacking most of its right side, the inter-zonal part and portions of the left lateral margin and of the left cornu. In addition to the holotype two small shield fragments (Pal. Mus. Oslo nos. A24902, A30000) are referred with hesitation to the same species.

Description. — On account of the poor state of preservation very few exact measurements could be taken; the distance of the pineal foramen from the rostral end of the shield is thus 42 mm. It is, however, evident that the shield is large, more than twice as great as that of *B. holtedahli* but distinctly smaller than that of *B. grandis*. The shield is also much flattened in its present condition, with the height amounting to only about 5—6 mm.

Although the cephalic shield is very imperfect, its shape could be restored with a fair degree of probability (fig. 79). The shield is very broad with the maximum breadth at least twice as great as the length of the shield in the median line, and probably considerably broader. The rostral margin is preserved, it is convex without any trace of a rostral angle and very probably passing into the lateral margins without

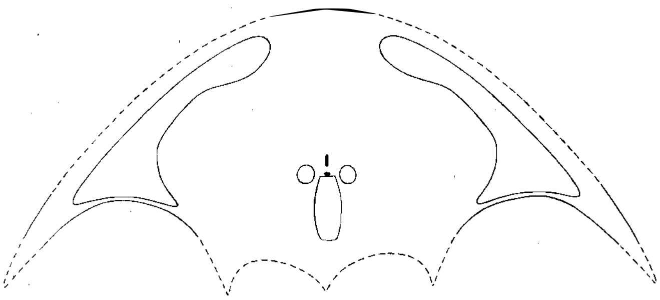


Fig. 79. — *Benneviaspis platessa* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (Pal. Mus Oslo no. A24901). About ½.

interruption by any antero-lateral angles. The lateral margins are somewhat curved. The cornua continue in the same direction as the lateral margins and project postero-laterally. They are long and slender, and their length is probably contained about two and a half times in the distance of their tips from the rostral end of the shield. The inner margin of the preserved basal portion of the cornu is devoid of denticles. The pectoral sinus is very broad and rather shallow; there is no antero-median but a faint antero-lateral corner in the sinus. The inter-zonal part of the shield is not preserved but seems to be of a moderate breadth. The dorsal sensory field is very small in proportion to the size of the shield and also feebly developed in comparison with the lateral fields. It is elongately oval in shape with truncated anterior and posterior margins; its length is twice as great as its maximum breadth (16 and 8 mm, respectively). The lateral fields are well developed, the anterior third of the fields is somewhat widened, in the middle part they are rather narrow. The posterior part of the fields has a postero-lateral triangular projection on to the basal part of the cornua and a somewhat narrower postero-median process reaching on over the zonal part in front of the pectoral sinus. The lateral fields are thus developed in the same way as those of *B. holtedahli*. The orbital openings are very small in proportion to the size of the shield; they are roundedly oval in shape and are situated far backwards, probably much behind the middle of the length of the shield in the median line. The circum-orbital ridge is very feebly developed. There is no independent pineal plate. The naso-hypophyseal opening is small and of about uniform breadth, its three divisions being hardly distinguishable; the posterior end of the opening lies on the anterior portion of a small elevation. The circum-nasal fossa is divided into two independent, elongate, rather deep grooves on each side of the naso-hypophyseal opening.

The exoskeleton is very poorly preserved. The superficial layer is probably continuous and its outer face is probably smooth in the main parts of the shield but on the circum-orbital ridge there are very small tubercles; the dorsal face of the cornu is ornamented with small lengthened tubercles and on the lateral margin the ornamentation consists of very delicate longitudinal ridges. There are no traces of any radiating canals to be detected in the middle layer. The mucous canal system was very probably developed as a very fine-meshed plexus and enclosed in the exoskeleton.

Only faint traces of some of the canal layers in the endoskeleton can be seen. We thus find that the canal sel_1 is branching at a point somewhat nearer to the lateral sensory field than to the orbit.

Remarks. — Although the specimen, on which this new species, *B. platessa,* is erected, is very imperfectly preserved, it shows some peculiar characters which will render the species rather easily recognizable. It differs from most of the described species in the size of its shield, and from *B. grandis* (p. 460) which it approaches in this respect, by the development of the sensory fields. Other peculiarities of *B. platessa* are the small orbital openings, situated far backwards, and the dorsal field, strikingly small compared with the well developed lateral fields.

Geological horizon. — Lower Eodevonian (Dittonian): Red Bay series, the Benneviaspis layer.

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis [W. side, 500—600 m], the Benneviaspis horizon (no. A24901; in the same piece of rock as *B. holtedahli,* no. A30006). — The specimens hesitatingly placed here were found on Mt Ben Nevis, in the horizon J (no. A24902) and the Benneviaspis horizon (no. A30000).

The specimens were all collected during Th. Vogt's expedition in 1928.

Benneviaspis sp. 1.

(Fig. 80; pl. 68:2.)

The form described below and designed as *Benneviaspis* sp. 1 is represented by a very fragmentary shield (Pal. Mus. Oslo no. A24899), which consists of the left side of a cephalic shield lacking portions of the inter-zonal part and the distal parts of the cornua.

Description. — Because of the imperfect state of preservation of the shield no exact measurements could be taken. The length of the shield (on the supposition that the posterior end of the shield reached backwards as far as the postero-lateral angles) can be estimated at about 32 mm, the maximum breadth at about 55 m, the posterior breadth of the inter-zonal part at 21 mm and the distance of the pineal foramen from the rostral end of the shield at 17 mm. In size the cephalic shield is thus comparable with that of *B. holtedahli, B. lankesteri* and *B. anglica,* and its general shape recalls that of *B. anglica.*

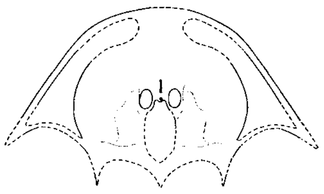


Fig. 80. — *Benneviaspis* sp. 1 . Attempted restoration of the cephalic shield in dorsal view; after Pal. Mus. Oslo no. A24899. ¾.

The very rostral end of the shield is not preserved and it is thus uncertain whether there was a slight rostral angle or not. At the transition between the rostral and the lateral margins there is a distinct obtuse angle. The lateral margins are straight. The distal parts of the cornua are not preserved so that their actual length can not be ascertained; it is, however, evident that the cornua are narrower and slenderer and more elongated than in *B. holtedahli,* and they thus recall those of *B. anglica.* The pectoral sinus are broad, but better defined than in *B. holtedahli,* and the specimen seems in this respect to occupy an intermediate position between *B. holtedahli* and *B. anglica.* The sensory fields are very imperfectly preserved so that their real shape cannot be determined. The dorsal field was probably rather broad, its most anterior part is narrow with the very anterior margin rather deeply emarginate just behind the pineal foramen. The lateral fields are very broad and provided with a strongly developed postero-median process, reaching over the zonal part in front of the pectoral sinus. The orbital openings are rather small and oval. No independent pineal plate is present. The naso-hypophyseal opening is narrow and very elongated.

The exoskeleton possesses a continuous superficial layer, and its outer face (as far as observed) it without any ornamentation. No radiating canals have been observed in the middle layer; in the lower division of that layer there is, however, a horizontal network of irregularly anastomosing vascular canals. The mucous canal system is enclosed in the exoskeleton and forms a fine-meshed plexus.

Some portions of the sensory line system are observed. It may be sufficient here to point out that the groove *mp* (cf. *B. holtedahli,* Stensiö 1927, fig. 76, *pc)* is well developed and rather long.

Remarks. — As far as comparisons are possible this form is rather suggestive of the British species *B. anglica* (Stensiö 1932, p. 156) in the general shape of its shield but differs i. a. by the shape of the dorsal sensory field. It also seems to fall outside the range of variation of *B. holtedahli* (p. 450; Stensiö 1927, p. 289). On account of the imperfect state of preservation of its shield, it does not exhibit many important characters, and it seems therefore most appropriate not to refer it to any of the known species nor to describe it as a new species but to place it as an undeterminable form of *Benneviaspis.*

Geological horizon. — Lower Eodevonian (Dittonian):

Red Bay series, the Ben Nevis division (in layers very probably corresponding to the Benneviaspis horizon, cf. Kiær & Heintz 1935, pp. 15—16).

Locality. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, N. W. side, between the First and Second Glaciers ("Tunge").

The specimen was collected in 1928 by Th. Vogt's expedition.

B. Species from the Wood Bay series.

4. *Benneviaspis lövgreeni* n. sp.

(Fig. 81; pl. 75:1.)

Diagnosis. — A *Benneviaspis* species of medium size with very broad cephalic shield. Lateral margins slightly convex with pronounced concavity at bases of cornua. Proximal parts of cornua directed laterally and slightly posteriorly. Pectoral sinus broad and shallow. Inter-zonal part rapidly narrowing backwards. Postero-lateral angles extending backwards somewhat behind posterior angle. Dorsal sensory field very broad, its breadth somewhat exceeding its maximum length; its most posterior part forming a small and narrow median process. Lateral sensory fields rather broad, extending in postero-median direction to a point somewhat in front of postero-lateral angles of inter-zonal part. Orbital openings situated near middle of length of shield in median line.

Holotype. — Cephalic shield (ENS no. 612).

Material. — Only one specimen, the holotype (ENS no. 612), is placed here; it consists mainly of the dorsal exoskeleton and parts of the left endoskeletal shoulder-girdle of a fragmentary cephalic shield, exposed in ventral view, and lacks the rostral end, most of the lateral parts on the right side, and the distal parts of the left cornu.

Description. — Owing to the imperfect state of preservation of the shield no accurate measurements can be given with the exception of the breadth of the inter-zonal part between the postero-lateral angles which is 35 mm. The length of the shield in the median line can be estimated at 42 mm. It is evident that the species was of medium size but larger than *B. holtedahli*.

The rostral margin is not preserved. The lateral margins are anteriorly very slightly convex but provided with a distinct concavity at the bases of the cornua. Only the most proximal part of the left cornu is preserved, projecting in a lateral and slightly posterior direction and thus forming an angle of about 70 degrees with the main axis of the shield. The pectoral sinus are broad and very shallow. The inter-zonal part is very broad but decreases rapidly in breadth backwards; its postero-lateral angles reach farther backwards than the posterior angle. The inter-zonal sinus are moderately deep and almost symmetrically

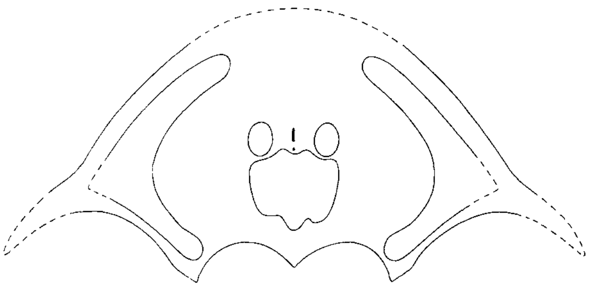


Fig. 81. — *Benneviaspis lövgreeni* n. sp. Attempted restoration of the cephalic shield in dorsal view. After the holotype (ENS no. 612). ¾.

concave. The dorsal sensory field is very broad, with its maximum breadth even somewhat greater than its length in the median line; it reaches almost as far laterally as the lateral margins of the orbital openings. The field extends forwards between the orbital opening with two small lobes on each side of the pineal foramen; posteriorly the field has a small narrow median process. The distance of the posterior end of this process from the posterior angle of the inter-zonal part is about half as great as the length of the field. The lateral sensory fields are of moderate breadth; they possess a lateral process extending to the basis of the cornua but the exact shape of this process cannot be ascertained; postero-medially the fields extend over the zonal part on to the inter-zonal part and end just in front of the postero-lateral angles in the same way as in *B. grandis*. The orbital openings are of medium size, roundedly oval in shape; they are situated about midway between the rostral and the posterior end of the shield. The naso-hypophyseal opening is very small and narrow, its posterior portion lies on a small elevation but the circum-nasal fossa is rather feebly developed.

Nothing can be said about the structure of the exoskeleton because of its poor state of preservation.

Of the internal endoskeletal structures some of the canals of the shoulder-girdle of the left side are displayed, i. a. the large marginal vein sinus which is situated rather far medially.

Remarks. — *B. lövgreeni* is named in honour of Captain H. Lövgreen of Norsholm (Sweden) who has given material assistance to several Swedish expeditions for the collection of vertebrate fossils.

The species resembles *B. grandis* in the development of the lateral sensory fields, and in this respect is very distinctly different from the other described species of the genus (with the possible exception of *B. maxima*). From *B. grandis* and *B. maxima* it is at once distinguished by the smaller size and the shape of the cornua.

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, lowermost part of the C. Kjeldsen division.

Locality. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, on the slope towards the Hoffnung Glacier.

The single specimen was collected by the ENS expedition in 1939.

5. *Benneviaspis grandis* n. sp.

(Fig. 82; pl. 73.)

Diagnosis. — A very large *Benneviaspis* species with maximum breadth of cephalic shield somewhat more than twice as great as length in median line. Rostral margin very obtuse, without rostral angle. More or less distinct antero-lateral angles present between rostral and lateral margins of shield; lateral margins almost straight or slightly convex. Cornua rather long and slender; their length contained about three times in distance of their tips from middle of rostral margin; projecting in postero-lateral direction; distal parts slightly curved backwards; inner margins without denticles. Pectoral sinus broad and shallow. Inter-zonal part rapidly narrowing backwards; postero-lateral angles reaching farther backwards than posterior angle. Dorsal sensory field broad, its maximum breadth in anterior part of field about as great as its length in median line; anterior margin deeply concave; posteriorly with narrow median posterior process. Lateral sensory fields broad, with triangular postero-lateral process on to basal parts of cornua, and continuing in postero-median direction to a point slightly in front of postero-lateral angles of inter-zonal part. Orbital openings far apart, situated in front of middle of length of shield in median line. Naso-hypophyseal opening between middle and posterior parts of orbital openings.

Holotype. — Cephalic shield (ENS no. 469).

Material. — The material placed in this species consists of the holotype (ENS no. 469) only it is represented mainly by the dorsal exoskeleton of an almost complete cephalic shield, exposed from the ventral side, which is only lacking the tips of the cornua. In addition to this specimen I place here with much hesitation a detached right cornu (Pal. Mus. Oslo no. B182, S II 108).

Description. — The dimensions of the cephalic shield are as follows: The length in the median line is 11 cm, the distance of the tips of the cornua from the middle of the rostral margin is estimated at about 16.5 cm. The maximum breadth, which lies between the tips of the cornua, is estimated at 24 or 25 cm. The breadth of the inter-zonal part between the postero-lateral angles is 7 cm. The distance of the pineal foramen from the rostral margin is 5.5 cm. It is thus evident that the species must have attained a very large size.

On a whole, the shield is very broad and flat, and its maximum breadth is a little more than twice as great as the length in the median line and about one and a half times as great as the distance of the tip of a cornu from the middle of the rostral margin. The rostral margin is truncatedly rounded without any rostral angle. At the transition between the rostral and the lateral margins there are distinct, though

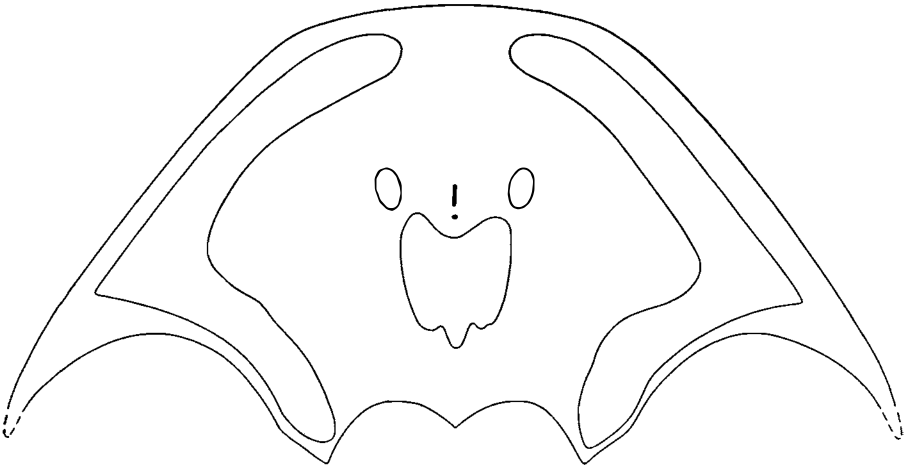


Fig. 82. — *Benneviaspis grandis* n. sp. Restoration of the cephalic shield, dorsal view, after the holotype (ENS no. 469). ½.

very obtuse, antero-lateral angles. The lateral margins are almost straight or very slightly curved. The cornua are rather long, and taper from a broad basis to a slender distal part. The length of the cornua constituted about, or somewhat more than, one-third of the distance of their tips from the middle of the rostral margin. They project in a postero-lateral direction and reached backwards about as far as the posterior end of the inter-zonal part; the distal parts of the cornua are slightly bent in a more posterior direction. The pectoral sinus are broad and rather shallow. The inter-zonal part is rather broad but narrows rapidly backwards, and its posterior breadth was contained somewhat more than three times in the maximum breadth of the shield. The lateral margins of the inter-zonal part are provided with an obtuse angle somewhat in front of the postero-lateral angles. These latter angles reach backwards to some distance behind the posterior angle. The dorsal sensory field is short and broad, somewhat broader in its anterior part than posteriorly; its maximum breadth is about equal to the length of the field in the median line. The anterior margin of the field is deeply emarginate; posteriorly the field has a narrow median process, recalling that in *B. holtedahli* but comparatively narrower and more pronounced than in this species. The distance of this process from the posterior end of the shield is about two-thirds of the length of the field in the median line. The lateral sensory fields are very strongly developed; they are broad, and end postero-laterally with an acute angle on the basal parts of the cornua. In postero-median direction the fields extend over the shoulder-girdle on to the inter-zonal part where they reach backwards to a point just in front of the postero-lateral angles. The orbital openings, which are of medium size and oval in shape, lie far apart, and the inter-orbital breadth is about four times as great as the transverse diameter of an orbital opening; they are situated in front of the middle of the length of the shield, and are also situated rather far in front of the anterior end of the dorsal sensory field. The pineal foramen, which is not situated in a separate plate, is placed far backwards, slightly behind the level of the posterior margins of the orbital openings. The narrow naso-hypophyseal opening is very small in proportion to the size of the shield; its anterior end lies distinctly behind the level of the anterior margins of the orbital openings; the circum-nasal fossa is very feebly defined.

The exoskeleton is very imperfectly preserved. The superficial layer is probably continuous; on the lateral portion of the circum-orbital ridge it is ornamented with small tubercles, on the other parts of the shield the outer face could not be observed. No radiating canals have been observed in the middle layer. The basal layer is rather thick and does not contain any ringsinus. •The mucous canal system is enclosed in the exoskeleton and very probably forms a fine-meshed plexus.

Of the internal endoskeletal structures only impressions of some canals are to be seen in the sensory fields.

Remarks. — *B. grandis* forms together with *B. lövgreeni* a distinct species group in the genus, differing from all other species so far described or known in this respect by the excessively developed lateral sensory fields. From *B. lövgreeni* (p. 458) it is easily distinguished by the size and the general shape of the shield. With regard to the size of its shield, *B. grandis* is comparable only with the somewhat larger *B. maxima;* it differs from this species, in which the shape of the posterior portion of the lateral sensory fields is almost entirely unknown, mainly by the shape of the anterior part of the shield, and of the dorsal sensory field, and by the posterior position of the naso-hypophyseal and pineal openings.

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, lowermost part of the C. Kjeldsen division.

Localities. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier (no. 469). Wood Bay: "at the head of the bay" (= same place as before; no. B182, doubtfully placed in this species).

The specimen no. 469 was collected by the ENS expedition in 1939.

6. *Benneviaspis maxima* n. sp.

(Fig. 83; pls. 74; 75:2.)

Diagnosis. — A very large *Benneviaspis* species with maximum breadth of the cephalic shield considerably more than twice as great as length of shield in median line. Rostral margin curved. No

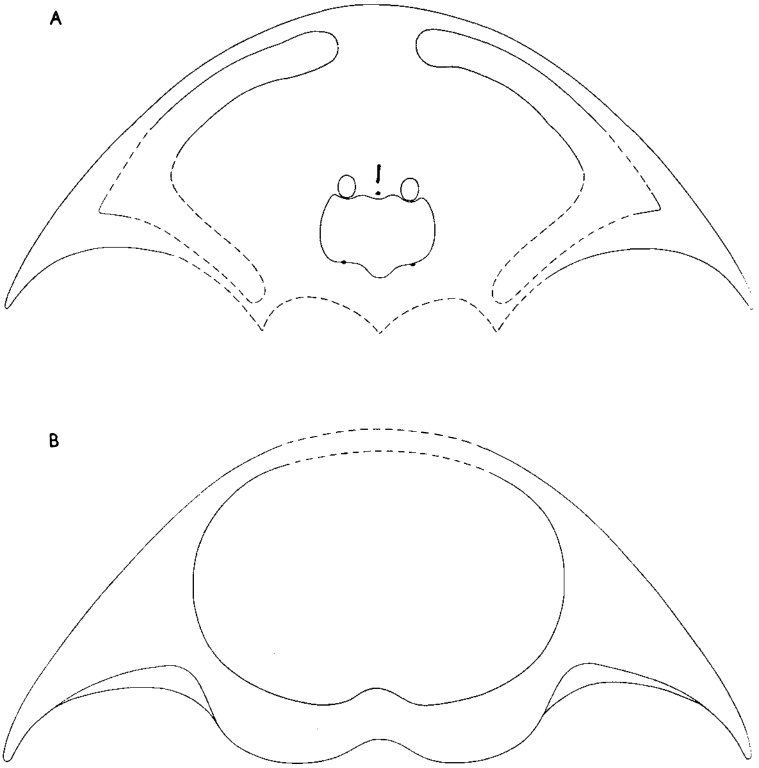


Fig. 83. — *Benneviaspis maxima* n. sp. Restoration of the cephalic shield, A, in dorsal view, combined after the holotype (ENS no. 471) and ENS no. 470; B, in ventral view, after ENS no. 470. ⅓.

antero-lateral corners at transition between rostral and lateral margins. Lateral margins slightly convex. Cornua rather long and slender; their length contained about three times in distance of their tips from rostral end of shield; projecting in postero-lateral direction, slightly curved; inner margins without denticles. Pectoral sinus very broad and shallow. Dorsal sensory field very broad, about one and a half times as broad as long; anterior margin undulate, posterior margin with broad, short, posterior process. Orbital openings situated behind middle of length of shield in median line. Anterior portion of naso-hypophyseal opening lying before level of anterior ends of orbital openings.

Holotype. — Fragmentary cephalic shield (ENS no. 471).

Material. — In this species two specimens (ENS nos. 470—471) are united. The holotype (no. 471, pl. 74) is a very fragmentary cephalic shield, wanting the lateral and posterior parts; no. 470 (pl. 75:2) consists of the ventral portion of the left side of a cephalic shield.

Description. — Owing to the imperfect state of preservation of the two shields few exact dimensions can be given. The distance of the pineal foramen from the rostral end of the shield is 7.3 cm. The maximum breadth is about 30 cm. The length of the shield in the median line is estimated to be approximately 12.5 cm. In size the shield is to be compared with that of *Cephalaspis gigas,* and it has thus belonged to a very large species.

In general shape the cephalic shield is very broad and its maximum breadth, which lies between the posterior ends of the cornua is very probably rather much more than twice as great as the length of the shield in the median line, and about one and a half times as great as the distance of the tip of a cornu from the rostral end of the shield. The rostral margin is well curved and, without any interruption of antero-lateral angles, passes gently into the lateral margins, which are slightly convex. The cornua are well developed, rather long and, in their distal parts, fairly slender, their length constituting about one-third of the distance of their tips from the rostral end of the shield; they project in a postero-lateral direction and probably reach backwards to about the same level as the posterior angle of the inter-zonal part; from no. 470 it is at least evident that they do not extend backwards behind the ventral portion of the inter-zonal part. The cornua are somewhat curved, and slightly more so in their distal parts but evidently not so much as in *B. grandis.* The inner margins of the cornua are devoid of denticles. The pectoral sinus are very broad and shallow, but as the posterior transverse wall of the zonal part of the shield is obliquely placed they are much deeper ventrally than dorsally. The pectoral sinus ventrally have a distinct antero-median corner. Very little can be said about the shape of the inter-zonal part; in the holotype almost nothing of it remains, and in no. 470 only its ventral portion is preserved. The inter-zonal part rapidly narrows posteriorly, its posterior breadth on the ventral side is contained about two and a half times in the maximum breadth of the shield; the breadth between the postero-lateral angles was very probable somewhat smaller. The posterior margin of the ventral portion of the inter-zonal part has a not very broad and shallow median concavity, and its anterior margin a corresponding anterior process towards the oralo-branchial fenestra. The dorsal sensory field is short and extremely broad; it is about one and a half times as broad as long, and reaches farther laterally than the lateral margins of the orbital openings. The anterior margin is undulate with sinuosities behind the orbital openings and the pineal foramen. Posteriorly the field has a short and broad median process. The lateral sensory fields are well developed, but the shape of their postero-median parts is entirely unknown. In postero-lateral direction they reach backwards to the basal parts of the cornua, and end here in an acute corner. The orbital openings, which are roundedly oval, are probably situated somewhat behind the middle of the length of the shield in the median line. The inter-orbital space is slightly more than twice as broad as the transverse diameter of an orbital opening. There is no independent pineal plate, and the pineal foramen is situated between the posterior parts of the orbital openings. The naso-hypophyseal opening is rather long and its anterior division reaches farther forwards than the orbital openings while the posterior division lies between the anterior parts of the orbits. The circum-nasal fossa is very shallow.

The exoskeleton is very imperfectly preserved. No ornament of its outer face has been observed. It seems very likely that the superficial layer formed a continuous covering to the middle layer on the whole shield. The basal layer is comparatively thick. The mucous canal system, after observation along the rostral margin of the shield, is enclosed in the exoskeleton and forms a very fine-meshed network of uniform and delicate canals.

Of the endoskeleton the linings of the superficial canals seem to be fairly well ossified but the state of preservation is in general very bad. The canal sel_1 branches at some distance medially to the lateral sensory field. The disposition of a fragment of the canal vls_3 is such that the canal must have joined the canal *vcl* behind the orbit. In the dorsal sensory field the nerve canals are ramifying into a great number of long and narrow branches.

Remarks. — As said before, the species is represented only by two fragmentary cephalic shields, and although the two shields exhibit no really remarkable characters which are common to both of them, they agree in size and general shape, and it seems thus likely that they both belong to one and the same species. Combined they give an approximate yet in many respects imperfect idea of the shape of the shield.

B. maxima is especially characterized by its large size, the broad cephalic shield with its rather slender cornua, and by the shape of the dorsal sensory field. From *B. grandis* (p. 460), which is only somewhat smaller than *B. maxima,* the latter species differs by the broader shield, by the shape of the rostral margin and of the dorsal sensory field. Unfortunately the lateral sensory fields are so imperfectly preserved, that nothing can be said about the shape of their postero-median parts, whether they were shaped as in *B. grandis* and *B. lövgreeni* or not, and it is thus uncertain if *B. maxima* belongs to the same species group as these species.

As noted before a *"Cephalaspis* sp.", mentioned by Stensiö (1927, p. 285; pl. 6:2), very probably belongs to *Benneviaspis;* the size and the details of the preserved part agree so well with those of *B. maxima* that it does not seem unlikely that the fragment really belongs to the species *B. maxima.*

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, lowermost part of the C. Kjeldsen division.

Locality. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier.

The two specimens (nos. 470—471) were collected by the ENS expedition in 1939.

Benneviaspis sp. 2.

(Fig. 84; pl. 72:1.)

The form, described below and designed as *Benneviaspis* sp. 2, consists of a very imperfectly preserved and somewhat distorted cephalic shield (Pal. Mus. Oslo no. D5808), which is weathered and abraded in such a way, that the outlines of the shield (but nothing of the most posterior parts) are indicated by preserved parts of the exoskeleton; the position of the orbits is also faintly indicated by the orbital ridges.

Description. — The distance of the tip of the right cornu from the rostral end of the shield is 44 mm and the distance of the anterior ends of the orbital openings from the rostral end of the shield is 11 mm; no other exact measurements could be taken. The maximum breadth of the shield, which lies between the tips of the cornua, is estimated at 60 mm and the length of the shield in median line and the breadth of the inter-zonal part are very roughly estimated at 30 mm and 22 mm respectively. It is thus evident that the specimen attained a moderate size, and was of about the same size as *B. holtedahli*.

The rostral margin is convex and comparatively narrow without any rostral angle, and passes into the more slightly curved lateral margins without any boundary. The cornua are long and slender, and slightly bent, they project in a postero-lateral direction and reach rather far backwards, probably at least as far as and possibly somewhat behind the posterior end of the shield; their length constitutes somewhat more than one-third of the distance of their tips from the rostral end of the shield. The pectoral sinus are broad but probably deep and well defined. The inter-zonal part is rather broad; its breadth is probably contained about two and a half times in the maximum breadth of the shield; its shape could not be determined but it is evident that the posterior margin between each of the postero-lateral angles and the posterior angle is concave (a feature characteristic of i. a. the genus *Benneviaspis)*. Nothing can be said about the shape of the dorsal sensory field. With regard to the lateral fields we can see of them some indistinct impressions, making it rather obvious that the fields extend postero-laterally over the basal parts of the cornua; postero-medially they reach at least over the zonal part in front of the pectoral sinus, but it seems rather unlikely that they extended on to the inter-zonal part. The orbital openings are situated strikingly far forward, probably very much in front of the middle of the length of the shield in the median line.

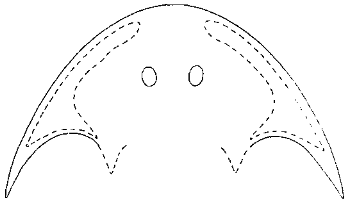


Fig. 84. — *Benneviaspis* sp. 2. Partial restoration of the cephalic shield in dorsal view. After Pal. Mus. Oslo no. D5808. ¾.

Remarks. — This form is too imperfectly preserved as to be adequately described and to be assigned a specific name, but it is almost certain that it can not pertain to any of the already described species, and that it represents a species of its own. With a very high degree of probability it is referred to the genus *Benneviaspis* on account of the general shape and proportions of the shield and the inter-zonal sinus as well as for the shape of the faint impressions of the lateral sensory fields. In the general shape and size of its shield it is very suggestive of *B. holtedahli* but differs from that species by the shape of the slender cornua and the very far anteriorly situated orbital openings.

Geological horizon. — Upper Eodevonian?: upper parts of the Wood Bay series.[1]

Locality. — Spitsbergen. At the head of Widje Bay, W. side, the passage (590 m) between Jäderin Valley and Zeipel Valley.

The specimen was collected by Th. Vogt's expedition in 1928.

Genus **Hoelaspis** Stensiö.

1927. *Hoelaspis,* Stensiö, p. 291.

Diagnosis. — A cephalaspid genus with broad and depressed cephalic shield. Anterior margin of cephalic shield protracted into pointed rostral process. Cornua very long and slender, projecting in lateral and somewhat anterior direction. Pectoral sinus shallow and ill-defined. Inter-zonal part broad and rather short, closed ventrally; posterior and postero-lateral angles protracted; inter-zonal sinus deep; dorsally without median ridge or spine. Sensory fields well developed, consisting of an unpaired dorsal and one pair of lateral fields; lateral fields extending over proximal part of cornua, with distinct postero-median angle on zonal part in front of pectoral sinus. No pineal plate.

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[1] The species in found together with the Arthrodires *Arctolepis decipiens* (?), *Actinolepis* sp., and *Monaspis acuticornis* (see Heintz 1929b). According to Føyn & Heintz (1943) the first of these species is characteristic of the Lyktan division, the genus *Actinolepis* "is probably characteristic of the upper part of the Lyktan division", and the last species belongs to a group of species, which is regarded as index-fossils for the Stjørdalen division. The *Benneviaspis* sp. 2 thus comes from the upper part of the Wood Bay series, and is by far the youngest *Benneviaspis* form as yet known.

First nerve canal for lateral sensory fields extending undivided at least as far as midway between orbit and lateral sensory field. Canal for r. mandibularis trigemini mainly lying behind canal of most anterior nerve for lateral sensory fields. Canal of dorso-lateral superficial vein 3 opening into canal of vena capitis lateralis behind orbit. Superficial layer of exoskeleton continuous. Middle layer without radiating canals. Mucous canal system enclosed in exoskeleton, forming fine-meshed network.

Type species. — *Hoelaspis angulata* Stensiö (1927, by monotypy).

Remarks. — The diagnosis of the genus, given by Stensiö (1927, p. 292) must be altered in consequence of the new facts brought forward by studying the in some respects more perfectly preserved material of the type species now present.

With regard to the disposition of the canal of the r. mandibularis trigemini (V_3) the statement in the diagnosis applies to the middle parts of this canal running near the dorsal face of the endoskeleton; most proximally the canal crosses the canal sel_1 on its ventral side, and distally it enters the oralo-branchial chamber very far laterally and below the posterior branch of the first nerve canal just mentioned.

The systematic position of the genus and its relationship to the other cephalaspid genera have been discussed by Stensiö, who (1927, pp. 291—292) considers it to be closely allied to *Benneviaspis, Boreaspis, Thyestes,* and *Kiaeraspis* on account of the inner anatomical characters; he also points out the likeness between *Hoelaspis* and the two first mentioned genera in the development of the lateral sensory fields. Later (1932, p. 152) Stensiö unites the genera *Benneviaspis, Securiaspis, Hoelaspis, Boreaspis,* and *Kiaeraspis* into a separate genus group in his sub-family "Kiaeraspinae".

Disregarding the shape of the lateral sensory fields, the close resemblance of *Hoelaspis* to *Benneviaspis* and *Boreaspis* is much more striking now that we have a better idea of the real shape of the cephalic shield in *Hoelaspis,* in particular with regard to the form of the inter-zonal part. In all these three genera the posterior margin of the inter-zonal part is strongly concave between the posterior angle and each of the postero-lateral angles, and this sinus reaches so far anteriorly that the exoskeletal component extends only rather inconsiderably *(Benneviaspis, Hoelaspis)* or almost not at all *(Boreaspis)* behind the endoskeletal component of the inter-zonal part. This character removes the mentioned genera from the closer affinity of *Kiaeraspis* (,*Axinaspis* and *Nectaspis*). *Hoelaspis* and *Boreaspis* have both a well developed rostral process; *Boreaspis* differs, however, from *Hoelaspis,* by other characters i. a. by the development of the lateral sensory fields. In the shape of the sensory fields *Hoelaspis* bears a strong likeness to *Benneviaspis,* in particular to *B. platessa, B. lankesteri, B. anglica* and *B. longicornis,* and in the general appearance of the shield it reminds among these species most closely of *B. longicornis.*

As is noted before (pp. 242, 447) it seems probable that *Hoelaspis* has developed from some species group in *Benneviaspis* and that it, in its turn, has given rise to the genus *Boreaspis.*

The genus contains at present one single species, *H. angulata.* It is confined to Spitsbergen, not being found elsewhere, and is here recorded from the upper parts of the Red Bay series; the genus is thus of Dittonian age.

Hoelaspis angulata Stensiö.

(Fig. 85; pls. 76—77.)

1927. *Hoelaspis angulata,* Stensiö, p. 292; fig. 77; pls. 44—46; 47:1.

Diagnosis. — Same as for genus (only species).

Holotype. — Cephalic shield (no. 89) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 292).

Material. — The new material of this species at my disposal consists of only four specimens (Pal. Mus. Oslo nos. A24896—A24898 and ENS no. 476). Two of them, nos. A24896 (pl. 76) and 476, are represented by nearly complete cephalic shields in counter-part; no. A24898 is a fragmentary shield with the ventral portion of the inter-zonal part, the post-branchial wall and parts of the dorsal exoskeleton exposed in ventral aspect. No. A24897 (pl. 77:2), a fragmentary shield, lacking the rostral process and most of the cornua, differs from the other specimens by slightly greater size, but as it exhibits no structural differences it too is referred to this species. — I have also had the opportunity to restudy the holotype shield (pl. 77:1).

Description. — The dimensions (in mm) of the cephalic shields are given in the following table (figures in brackets are only approximate):

Nos.	A24896	A24897	A24898	476
Maximum breadth	36	—	(40)	(33)
Breadth of inter-zonal part, posteriorly	11	13.5	(11)	10
Length in median line	16.5	—	—	19.5
Distance between basis of rostral process and posterior end of inter-zonal part	12	15	—	13.5
Distance of pineal foramen from posterior end of shield	6.2	(8)	—	(7)

For detailed information on the species, the reader is referred to the original description by Stensiö (1927, pp. 293—294). In the following only an amplifying description is given, leaving out of consideration such characters in the new material that are in agreement with the original description.

The maximum breadth of the shield, which lies between the tips of the cornua, is somewhat variable according to the different length of the cornua, being from somewhat less to slightly more than twice as great as the length of the shield in the median line.

The main shield (thus the shield exclusive of the cornua and the rostral process) is distinctly broader than long. The rostral margin is protracted into a fairly long rostral process in the form of a narrow sharply pointed triangle; the length of the rostral process is contained about three to three and a half times in the distance of its apex from the posterior end of the shield. The antero-lateral margins of the shield are slightly convex but there is no distinct angle. The cornua are very long, they are broad in their proximal parts but as a whole very slenderly built; in the most distal parts they are slightly bent backwards so that the tips of the cornua point in a straightly lateral direction; the cornua are thus very faintly sigmoidally bent. The length of each cornu is somewhat variable but is in general about equal to the breadth of the inter-zonal part between the postero-lateral angles. The posterior margins of the cornua are devoid of denticles. The inter-zonal part of the shield which rapidly narrows backwards, has posteriorly protracted postero-lateral and posterior angles; the posterior angle projects somewhat behind the postero-lateral angles. The inter-zonal sinus are deep, and asymmetrically developed with their deepest part situated antero-laterally, almost in front of the postero-lateral angles. The shape of the inter-zonal part reminds rather much of that in *Benneviaspis longicornis*. The ventral portion of the inter-zonal part is closed, forming a rather narrow transverse bridge, which laterally is somewhat broader than in the middle of its breadth; medially its posterior margin has a rather small, almost semi-circular concavity. The dorsal sensory field is very elongate and reversely ovate, about three times as long as broad with its maximum breadth somewhat posterior to the middle of its length; anteriorly it is tapering to a narrow point lying immediately behind the pineal foramen; posteriorly the field is sharply rounded. The openings for the ductus endolymphatici are situated near the posterior end of the field at its very border or immediately laterally to it. The distance of the posterior end of the field from the posterior end of the inter-zonal part is about half as great as the length of the field. The lateral sensory fields do not extend in lateral direction beyond the first third of the length of the cornua. The orbital openings lie at about equal distance from the basis of the rostral process and from the posterior end of the shield (nos. A24896, 476). There is no pineal plate. The inter-orbital breadth is about as great as the transverse diameter of an orbital opening. The naso-hypophyseal opening is very elongated; the circum-

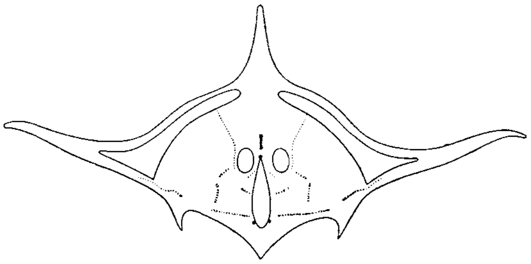

Fig. 85. — *Hoelaspis angulata* Stensiö. Restoration of the cephalic shield, dorsal view. After ENS no. 476 and Pal. Mus. Oslo no. A24896. × 2.

nasal fossa is very slightly developed and only somewhat deeper around the anterior division of the naso-hypophyseal opening than posteriorly.

The observed grooves of the sensory line system are indicated in fig. 85 (except the infraorbital line which is inserted after Stensiö 1927, fig. 77).

The superficial layer of the exoskeleton is in the main parts of the shield continuous and smooth without any ornamentation; on the cornua, however, its outer face is provided with very delicate longitudinal ridges, running parallelly to the margins of the cornua, and it is very probable that the vascular canals in the middle layer are also disposed in rows corresponding to the superficial ridges. In the main cephalic shield there are in the lower division of the middle layer irregularly branching and anastomosing, horizontal canals, evidently corresponding to the radiating vascular canals in other Cephalaspids. The mucous canal system (pl. 77:1) is made up of a rather irregular and not very fine-meshed network of canals of somewhat varying calibre: it is thus not differentiated into circum-areal and intra-areal canals.

Several of the internal cavities and canals are displayed in nos. A24896 and A24897 and in the main parts seem to correspond to those in the beautifully preserved specimens figured by Stensiö (1927, pls. 44—46; 47:1). In no. A24897 (pl. 77:2) the canal sel_1 on the left side runs undivided only as far as to a point about midway between the orbit and the lateral field. In the same specimen the canal vls_3 runs in such a direction that it will open into the canal *vcl* immediately postero-laterally to the orbit; the canal vls_4 opens directly into the canal *vcl* whereas the canals vls_5 and vls_6 join rather laterally into a long common trunk which also receives a well developed canal vls_7.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series, the Ctenaspis and Benneviaspis horizons.

Localities. — Spitsbergen. E. side of Red Bay: Mt Ben Nevis, [W. Plateau, 500—600 m], in the Benneviaspis horison (nos. A24896—A24898); W. side of Wood Bay: Mt Sigurd, S. W. part, slope towards the Hoffnung Glacier (no. 476).

Nos. A24896—A24898 were collected by Th. Vogt's expedition in 1928, no. 476 by the ENS expedition in 1939.

Genus **Boreaspis** Stensiö.

1927. *Boreaspis,* Stensiö, p. 294.

Diagnosis. — A cephalaspid genus with main cephalic shield anteriorly provided with rostral process of varying length and laterally with cornua of varying shape and size. Pectoral sinus more or less well defined. Inter-zonal part broad and rather short, ventrally closed, dorsally without median ridge or spine; posterior and postero-lateral angles protracted backwards; with inter-zonal sinus. Sensory fields well developed, consisting of an unpaired dorsal and one or two pairs of lateral fields; lateral fields not extending on to cornua, continuing backwards on to dorso-lateral sides of inter-zonal part. No pineal plate. First nerve canal to lateral sensory field running undivided to median margin of lateral field or, more rarely, to a point about midway between orbit and lateral field. Canal for r. mandibularis trigemini situated immediately behind first nerve canal for lateral sensory field. Canal for dorso-lateral superficial vein 3 opening into canal of vena capitis lateralis behind orbit. Superficial layer of exoskeleton generally continuous. Middle layer without radiating canals. Mucous canal system generally enclosed in exoskeleton, forming a fine-meshed network.

Type species. — *Boreaspis rostrata* Stensiö (1927, by monotypy).

Remarks. — With regard to its general shape the main cephalic shield is more or less rounded or diamond-shaped. Dorsally it is much depressed and only slightly raised in its postero-median parts, the height of the shield is thus very inconsiderable and the shield reminds in this respect much of that in *Benneviaspis, Hoelaspis,* and *Ectinaspis.* The shield is provided anteriorly with a rostral process of varying length, in some species (e. g. *B. curtirostris)* very short (even shorter than in *Hoelaspis angulata),* in others (e. g. *B. batoides, B. macrorhynchus)* almost equalling the length of the main shield. The cornua are of varying length and shape; they issue from the main shield at about the middle of its length, in one species *(B. ceratops)* however, considerably anterior to this point, and project in a lateral or postero-lateral direction, never straight posteriorly; they do not reach backwards far behind the level of the posterior corner of the inter-zonal part even in those species where they are best developed (e. g. *B. curtirostris, B. gracilis, B. circinus).* The cornua are never provided with denticles on their posterior or lateral margins as is the case in many *Cephalaspis* species. The inter-zonal part is comparatively broad and short, and exhibits no apparent traces of segmentation; the inter-zonal sinus is asymmetrically developed with the deepest part of the concavity lying nearer to the postero-lateral than to the posterior angle; the exoskeletal component of the dorsal portion the inter-zonal part does not reach backwards (or only very slightly so) behind the endoskeletal component. As in *Benneviaspis, Hoelaspis* (and *Ectinaspis)* the inter-zonal part in *Boreaspis* never shows any sign of a median dorsal crest or ridge. The sensory fields are rather well developed. Contrary to what is the case in the preceding genera the number of lateral fields is not constant in the genus nor even within the species (as in *B. curtirostris).* Ordinarily there is one pair of lateral fields but the field on each side can be subdivided into two parts, separated from each other by an interval of varying breadth *(B. spinicornis, B. triangularis, B. circinus,* and in some specimens of *B. curtirostris).* The lateral fields do not reach backwards on to the cornua and there is not even a trace of a lateral angle or projection on to the base of the cornua; in this respect *Boreaspis* differs clearly from *Benneviaspis* and *Hoelaspis.* Backwards the lateral fields or the posterior pairs of the lateral fields continue postero-medially over the zonal part on to the inter-zonal part of the shield and reach backwards on its dorso-lateral sides to a point just anteriorly to the postero-lateral corners. A separate pineal plate is not developed in any of the species. The nasal opening consists of its usual three divisions of which the two anterior ones are often rather indistinctly separated from each other forming a fairly broad slit, whereas the posterior division is almost circular.

With regard to the inner anatomical characters of the genus the following may be noted. The canal sel_1 continues outwards to the extreme median margin of the field before branching (the most anterior branch is by far the strongest) or, exceptionally, branches at a point about midway between the orbit and the field. In the species in which the lateral field is divided into two portions the anterior one is supplied with two and the posterior one with three nerve canals. The canal V_3 crosses the first nerve canal of the lateral sensory field on its ventral side just laterally to the orbit and then runs antero-laterally in the visceral endoskeleton behind that canal before it opens rather far laterally into the oralo-branchial chamber, ventrally to the posterior branch of the canal sel_1. The canal vls_3 has been observed in only a few species in which it was seen to enter the canal *vcl* behind the orbit, and it is probable that this fact holds good for all the species and is characteristic for the genus. With regard to the visceral endoskeleton it can furthermore be observed that in relation to the endocranium and compared with the conditions in *Cephalaspis* it has shifted more or less forwards. No velar ridge is developed. The canal for the paired common efferent artery opens directly into the aortal canal. There are impressions of only seven branchial pouches. It must also be mentioned that in all species of *Boreaspis* the endoskeleton is completely ossified, consisting of cancellous bone lined with periosteal bone layers externally, and in the cavities and canals.

The superficial layer of the exoskeleton apparently forms a continuous covering to the middle layer; in some species *(B. costata* and some specimens of *B. robusta)* it seems, however, in some places to be extremely thin or even absent. The outer face of the exoskeleton is generally quite smooth without any ornamentation except on the main shield and on the rostral process in *B. costata* and in some specimens of *B. robusta,* as well as on the distal parts of the rostral process in some other species, where an ornamentation of small tubercles occurs, and on the tip of the cornua in *B. triangularis* and *B. curtirostris* which are provided with denticle-like tubercles. The middle layer exhibits no traces of any regularly disposed radiating canals, only a network of anastomosing vascular canals in the main shield. The basal layer contains no ringsinus. The structure of the exoskeleton is on the whole very similar in the genera *Boreaspis, Hoelaspis* and *Benneviaspis.*

The genus *Boreaspis* is obviously most closely related to *Hoelaspis* and *Benneviaspis.* It shares with these genera the general flattened shape of the shield without any dorsal median crest or ridge and the inter-zonal part with a rather deep inter-zonal sinus. The conditions of the canal sel_1, and of the disposition of the canal V_3 in relation to it as also the development of the exoskeleton and of the mucous canal system are furthermore similar in all the three genera. *Boreaspis* agrees with *Hoelaspis* in having a distinct rostral process but differs from the same genus by the development of the posterior portion of the lateral sensory field or fields; in this latter respect *Boreaspis* resembles some of the species of *Benneviaspis (B. grandis, B. lövgreeni)* with a strong postero-median process of the lateral field on to the inter-zonal part. It is perhaps deserving of note that a similar variation in the development of the lateral sensory fields, which occurs between the different species of the genus and also within the same species *(B. curtirostris),* is known to occur also in *Kiaeraspis,* a genus apparently not akin to *Boreaspis.* The genera *Hoelaspis* and *Boreaspis* are in fact so similar that the former can be regarded, if not as the actual precursor to the latter, at least as very closely related to this ancestor.

The genus *Boreaspis,* which was based on a single species, *B. rostrata,* today includes no less than thirteen species. They are the following:

B. batoides n. sp.
B. ceratops n. sp.
B. circinus n. sp.
B. costata n.sp.
B. curtirostris n. sp.
B. gracilis n. sp.
B. intermedia n. sp.
B. macrorhynchus n. sp.
B. puella n. sp.
B. robusta n. sp.
B. rostrata Stensiö.
B. spinicornis n. sp.
B. triangularis n. sp.

Within the limit of the genus these species represent a variety of different forms; they differ from each other to a varying degree and many of them can be classed together with their supposed allies in separate but not clearly defined species groups. *B. costata, B. robusta,* and *B. puella* form one group of allied species characterized by the very small triangularly shaped cornua and, as a consequence thereof, the laterally open pectoral sinus, the well developed rostral process, and the generally comparatively narrow cephalic shield. The second species group including *B. spinicornis, B. circinus,* and *B. triangularis* is characterized by the division of the lateral sensory field into two distinctly separated portions, and by the well developed postero-laterally directed cornua; *B. spinicornis* shows, however, points of connection with *B. curtirostris,* and *B. triangularis* with *B. rostrata.* A third species group is formed by *B. curtirostris* and *B. gracilis,* which are two closely related species, differing mainly in the development of the rostral process. In *B. curtirostris* the lateral sensory field is sometimes narrowed in the middle of its length and may even show a slight interruption, a feature pointing to the more advanced conditions in the preceding group. *B. macrorhynchus* is apparently more closely akin to *B. batoides* than to any of the other species and both these species may form a fourth species group. *B. rostrata* shows resemblances in the general configuration of its shield both with *B. macrorhynchus* and with *B. triangularis. B. intermedia* is imperfectly known but seems to resemble both *B. robusta* and allies and *B. macrorhynchus. B. ceratops* occupies a more isolated position and cannot be put in close relation to any of the previous groups.

The genus *Boreaspis* is only known from Spitsbergen, and is here confined to the lower and middle parts of the Wood Bay series. It makes its appearance with a diversity of forms in the lowermost part of the C. Kjeldsen division of the Wood Bay series; many species are restricted to that part, viz. *B. batoides, B. ceratops, B. puella,* and *B. rostrata;* others are also found in the upper part of the same (but not in the next) division, viz. *B. intermedia* and *B. macrorhynchus.* In this upper part appear as new species *B. circinus, B. robusta, B. spinicornis,* and *B. triangularis,* and of these *B. robusta* and *B. spinicornis* continue upwards into the Lyktan division *(B. spinicornis,* however, only in one locality, Mt Lyktan); *B. robusta* is common in this middle division of the Wood Bay series and is also met with in layers belonging to the uppermost part of the Lyktan division. *B. robusta* has thus a rather wide stratigraphical range. As a rule, however, the *Boreaspis* species have only a restricted vertical distribution.

1. *Boreaspis robusta* n. sp.

(Fig. 86; pls. 78—81; 117:2-3).

Diagnosis. — A *Boreaspis* species of medium size with maximum breadth of cephalic shield from slightly less to somewhat more than length of main shield (from basis of rostral process to posterior end of inter-zonal part). Rostral process well developed, of varying length, its length being from about one half to three-fourths as great as length of main shield in median line. Antero-lateral margins of shield curved. Cornua very small, triangular, with pointed apex, situated at posterior third of length of main shield, projecting in postero-lateral direction. Pectoral sinus shallow and rather ill-defined. Inter-zonal part very broad, its posterior breadth more than half as great as maximum breadth of shield. Posterior angle projecting backwards beyond postero-lateral angles. Dorsal sensory field elongately trapezoidal in shape, about twice as long as broad, broadest in posterior third or quarter of its length. Lateral sensory fields undivided, somewhat curved at basis of cornua. Orbital openings oval, situated slightly behind middle of length of main shield. Exoskeleton ornamented with very small tubercles at margins of shield and at apex of rostral process.

Holotype. — Cephalic shield (ENS no. 81).

Material. — The material which I refer to this species consists of no less than 150 specimens, Pal. Mus. Oslo nos. A24873 and A24874 (pl. 79:1), and ENS nos. 1—148. Three specimens, ENS nos. 149 (pl. 81:2), 150—151, are too imperfectly preserved to be definitely determined and are placed here with some hesitation.

All specimens consist of cephalic shields, often in a rather imperfect state of preservation. The specimens from the E. side of Mt Kronprinz are sometimes well preserved with regard both to their completeness and to the endoskeletal details but are often slightly distorted, e. g. nos. 1 (pl. 79:2), 8 (pl. 81:1), 12 (pl. 80:2), 21, 29, 31; those from Mt Borgen, nos. 118—142, 143 (pl. 80:1), 144—147, are for the most part well preserved as far as completeness is concerned, the endoskeleton is, however, in a poor state of preservation; this applies also to most of the specimens from Mt Lyktan and Mt Rebbingen. The holotype (no. 81, pl. 78:2-3) and no. 82 (pl. 78:1), are on the other hand, well preserved; both come from the same locality on Mt Lyktan as the holotype of *Nectaspis areolata* (cf. p. 542). The material from Mt Triplex is very poorly preserved and that from Mt Sørli is much distorted by pressure of the rock.

Description. — In order to show the dimensions of the shield and their variation in specimens from different localities the following table is given. The specimens, suitable for measurements, are

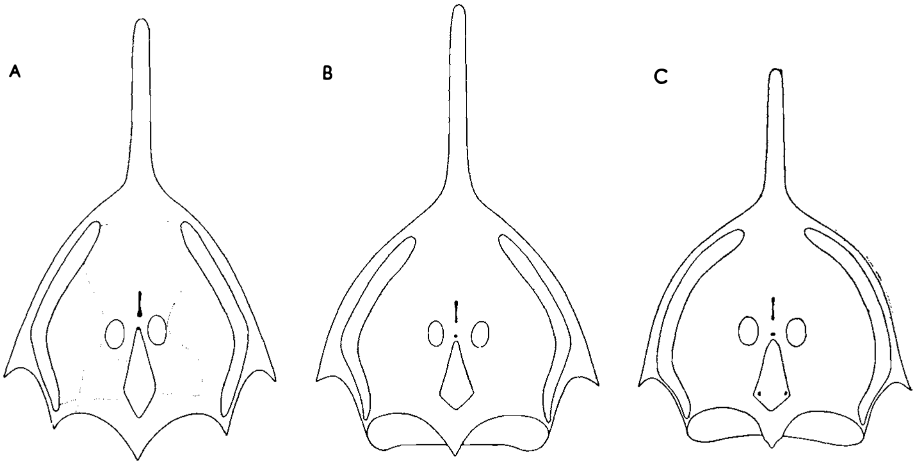

Fig. 86. — *Boreaspis robusta* n. sp. Restorations of three different cephalic shields in dorsal view, A, after ENS no. 1, B, mainly after ENS nos. 133 and 144, C, after the holotype, ENS no. 81. × 2.

divided into nine groups after their localities, and the following dimensions have been measured, viz. the length of the main shield from the basis of the rostral process to the posterior end of the inter-zonal part *(1)*, the maximum breadth of the shield between the tips of the cornua *(2)*, the length of the rostral process *(3)* and the breadth of the inter-zonal part between its postero-lateral angles *(4)*. The measurements are generally given as arithmetical means, and the range is expressed only by the extreme values (figures in brackets). In each case the numbers of the measurements are stated *(n)*. The dimensions are in mm. The localities are: *a*, Mt Kronprinz, E. slope; *b*, Mt Kronprinz, W. slope; *c*, Mt Barmfjellet; *d*, Mt Scott Keltie; *e*, Mt Errol White; *f*, Mt Lyktan; *g*, Mt Rebbingen; *h*, Mt Triplex; *i*, Mt Borgen.

	n	1	n	2	n	3	n	4
a	7	(16.9) 18 (19.0)	20	(15) 17.4 (20)	11	(9.5) 11.9 (16.5)	15	(9.2) 10.5 (11.5)
b	1	16.2	2	(14.5) 14.7 (15)	—	—	2	(8.8) 9.6 (10.3)
c	—	—	1	18	—	—	1	10.5
d	3	(15.7) 15.9 (16.3)	12	(15.5) 18 (21.4)	2	10.8 — 10.9	10	(9.7) 11 (13.4)
e	4	(18) 19.9 (21)	9	(18) 19.6 (22)	1	11.5	5	(11) 12.8 (14.9)
f	10	(15) 17 (19)	15	(14) 17.1 (19.5)	8	(8.3) 11.9 (17)	13	(9.8) 11.4 (13)
g	4	(16.8) 17.9 (18.9)	4	(18) 19 (20)	3	(12.4) 13.7 (14.8)	5	(10.7) 11.6 (12.9)
h	1	19.9	7	(15) 17.1 (21)	1	14	4	(10.2) 11.2 (12)
i	11	(15.5) 17 (19.6)	23	(15) 17.5 (21)	14	(9) 12.1 (14.8)	16	(10) 11.3 (13.5)

As in seen from the table the shield is rather variable in size even in specimens from the same locality; on the whole the differences between the shields from different localities are rather insignificant, and the proportions seem to be comparable. As there are no well marked differences in the shape of the shield or in any other character it seems very probable that all the specimens belong to one species, which, although fairly variable and possibly not homogenous, cannot (at least at present) be split up into distinct varieties.

The length of the cephalic shield from the apex of the rostral process to the posterior end of the inter-zonal part varies from 24.5 mm to 34 mm. The length of the main cephalic shield is seen to range from 15 mm to 21 mm, the mean being 17.5 mm ($n = 41$); the breadth between the tips of the cornua ranges from 14 to 22 mm, with a mean of 17.8 mm ($n = 93$); the breadth of the inter-zonal part between the postero-lateral angles varies from 8.8 mm to 14.9 mm (mean = 11.2 mm, $n = 71$).

Compared with the other species of the genus *B. robusta* must have attained a medium size.

The general shape of the main shield is somewhat variable. but most often it is of the shape displayed in fig. 86B—C, and is thus rather robust and fairly rounded, more rarely of this shape in the specimens from the locality on the E. side of Mt Kronprinz, that is, in the geologically oldest specimens, where it is more slenderly built and triangular as in fig. 86A. The maximum breadth of the shield, which lies between the tips of the cornua, is slightly greater than the length of the main shield in the median line. The rostral process is always well developed but very variable in length; in the holotype it is notably short, and attains only somewhat more than half of the length of the main shield, but in no. 89 it is about twice as long as in the holotype; in general it seems to be at most three-fourths as long as the main shield; the process is of about uniform breadth throughout its length and the tip is rounded. The antero-lateral margins of the shield are in most specimens well curved, more rarely, as in no. 1 (pl. 79:2; fig. 86A) they are only slightly convex. The cornua are very small, triangular in shape with narrow bases, and somewhat drawn out into a kind of point and projecting in a postero-lateral direction; they issue from the main shield at the beginning of the posterior third of its length. Proportionally the cornua are thus of the same size as in *B. puella* and *B. costata.* The pectoral sinus are rather shallow and narrow but facing laterally and thus asymmetric in shape. The inter-zonal part is rather long and very broad; it decreases slightly in breadth backwards and its breadth between the postero-lateral angles is always greater than half of the maximum breadth of the shield, and is in some specimens as great as two-thirds of this breadth. The posterior angle is of varying shape and is protracted backwards to a varying degree but always behind the level of the postero-lateral angles and generally farther backwards than the ventral region of the inter-zonal part. The inter-zonal sinus is moderately deep. The posterior margin of the ventral region of the inter-zonal part is slightly concave and this region reaches, on the whole, behind the postero-lateral angles but not as far backwards as the posterior angle. The dorsal sensory field is elongatedly trapezoidal in shape, that is, its greatest breadth lies in the posterior half, and from this point the field tapers, with almost straight lateral margins, gently towards its pointed anterior end, and narrows posteriorly much more abruptly towards the posterior end. The posterior margin is thus angulated, forming a right or an acute angle. The posterior end of the field lies at the same, or slightly before, the level of the inner end of the inter-zonal sinus. The shape of the field is somewhat variable, being narrower in some specimens than in others; its breadth is generally twice, sometimes two and a half times as great as its median length. Laterally the field is bordered on each side by an often rather distinct ridge, running from a point somewhat behind the anterior end of the field along the lateral margins on to the level of the posterior corners. The lateral sensory field on each side of the shield is undivided; it is of a slightly varying shape but generally distinctly broader in its anterior part than more posteriorly. The field is more or less distinctly bent at the basis of the cornu, the flexure of the field lying in some specimens more anteriorly at the anterior part of the basis of the cornu, in others more posteriorly and nearer to the pectoral sinus. The orbital openings are of a moderate size, oval in shape, and situated slightly behind the middle of the length of the main shield in the median line. The pineal foramen lies in some specimens between the middle parts, in others between the posterior parts of the orbital openings, in some specimens at the anterior end of the dorsal sensory field, in others again somewhat in front of this field. The naso-hypophyseal opening is normally developed, its posterior end lies at about the level of the anterior margins of the orbital openings. The circum-nasal fossa is triangular in shape but not well defined.

In most of the specimens the outer face of the exoskeleton is on the whole quite smooth, only at the margins of the shield and near the apex of the rostral process some very small tubercles are observed. In no. 82 the whole dorsal face of the shield is, however, ornamented with very small, closely set tubercles. The mucous canal system, enclosed in the exoskeleton, forms a fine-meshed network. The thin inner division of the middle layer contains the vascular canals which are developed as a network and not as radiating canals.

The sensory line system is observed in only a few specimens. It forms very delicate grooves in the exoskeleton; the lines observed in no. 1 are shown in fig. 86A.

The endoskeleton seems to have been well ossified but is most often badly preserved. In the holotype the canal sel_1 on the right side branches rather far proximally, but on the left side, and, as far as observed, in all other specimens it runs undivided to a point just medially to the lateral sensory field; in the holotype the canals vls_3 and vls_4 join into a short common trunk behind the orbit.

Remarks. — *B. robusta* together with *B. costata* (p. 483) and *B. puella* (p. 481) forms a distinct species group in the genus, characterized mainly by the feeble development of the cornua. The shield in *B. robusta* is intermediate in size between the larger *B. costata* and the smaller *B. puella;* from the first species it differs furthermore by the shorter inter-zonal part (or by the posterior attachment of the cornua), and by the shape of the dorsal sensory field, from the second species by the narrower bases of the cornua, the shape of the dorsal sensory field and of the inter-zonal part.

B. robusta is the commonest species of *Boreaspis,* occurring mainly in the middle division of the Wood Bay series, and is recorded from a large number of localities; it is, however, remarkable that it is unknown from the localities at Ekman Bay.

Geological horizon. — Upper Eodevonian (?): Wood Bay series, the C. Kjeldsen division (not in the lowermost part) and the Lyktan division.

The specimens from the localities at Mt Sørli come from layers, the exact position of which is not known, but which must belong either to the uppermost part of the Lyktan division or to the lowermost part of the Stjørdalen division.

Localities. — Spitsbergen. W. side of Wood Bay: Mt Kronprinz, E. side, opposite Stjørdalen Valley, in a grey sandstone (nos. 1—40). E. side of Bock Bay: Mt Kronprinz, W. slope (nos. 41—43). E. side of Wood Bay: Mt Scott Keltie, S. side (nos. 46—57, 60), S. part, W. slope (nos. 45, 58—59); Mt Sørli, in talus (nos. 61—63), Mt Sørli (= "between V. Stjørdalen and V. Verdalen"), 0—500 m (nos. 64—70). W. side of Wijde Bay (West Fiord): Mt Errol White, N. part, E. slope, fossiliferous horizon about 125 m (nos. 71—80), Mt Errol White (= "the Mtn S. of V. Sneugledal"), without closer indication of locality (nos. A24873—A24874). E. side of West Fiord: N. of Jørgensen Valley (no. 148). E. side of Dickson Bay: Mt Triplex, N. side (nos. 107—117); Mt Lyktan, S.E.slope (nos. 81—89, 98, 100), S.W.slope (nos. 90—91, 99), Fiskedalen Valley (nos. 92—97); Mt Rebbingen (= "the Mt. N. of Fiskedalen"), S.W.slope (nos. 101—106). N. of Dickson Bay: Mt Barmfjellet (no. 44). W. side of Dickson Bay: Mt Borgen, N. part (nos. 118—147).

The specimens nos. A24873—A24874 were collected by Th. Vogt's expedition in 1928, all the others by the ENS expedition in 1939.

2. *Boreaspis puella* n. sp.

(Fig. 87; pls. 82—83; 87:2.)

Diagnosis. — A *Boreaspis* species of small size with maximum breadth of cephalic shield as great as, or somewhat less than length of main shield (from basis of rostral process to posterior angle of inter-zonal part). Long rostral process; its length constituting from about one half to $^3/_5$ of length of main shield in median line. Antero-lateral margins of shield feebly curved. Cornua very small, triangular, projecting laterally and slightly posteriorly, situated at posterior third of length of shield. Pectorial sinus shallow and ill-defined. Inter-zonal part broad and rather long, rapidly narrowing backwards, posterior angle projecting backwards beyond postero-lateral angles; inter-zonal sinus deep. Breadth of inter-zonal part across postero-lateral angles at least half as great as maximum breadth of shield. Dorsal sensory field oval, about three times as long as broad, reaching far backwards, posterior margin truncated. Lateral sensory field undivided, more or less distinctly inflected at basis of cornua. Orbital openings situated about midway between basis of rostral process and posterior angle of inter-zonal part.

Holotype. — Cephalic shield (ENS no. 152).

Material. — The material referable to this species consists of twelve specimens, ENS nos. 152 (pl. 82:2, 4), 153—155, 156 (pl. 82:1), 157 (pl. 82:3), 158 (pl. 83:1), 159 (pl. 83:2), 160—163; all these are represented by cephalic shields, most of them in a more or less imperfect state of preservation. In addition to these specimens I place here with a slight hesitation one specimen, ENS no. 164, and with still more doubt another specimen, ENS no. 165.

Description. — The dimensions in mm of some of the shields are as follows (figures in brackets are approximate):

Nos.	152	155	156	157	158	159	160	163
Length of main shield	12.5	13.4	—	13.6	—	—	—	11.8
Maximum breadth	(12.5)	(12)	12.6	11	11.5	11.7	(10.5)	(10.5)
Posterior breadth of inter-zonal part	7	(6.5)	(7)	6.2	(6.5)	(7)	—	6
Length of rostral process ..	—	—	6.8	8	7.5	6.7	7	6.6

The other shields are too imperfectly preserved as to allow direct measurements to be taken but seem to be of approximately the same size as the measured shields. The two shields (nos. 164—165), hesitatingly placed here, are also very imperfect but seem to be slightly broader than the other shields. The species was thus of very small size.

The cephalic shield has a rather characteristic, narrow triangular shape, the antero-lateral margin forming a very acute angle with the main axis of the shield. The maximum breadth of the shield (between the tips of the cornua) does not exceed the length of the main shield in the median line. The length of the rostral process is distinctly less than the length of the main shield in the median line, in some specimens apparently only slightly more than half as long but in others about three-fifths as long. Viewed from above it is about parallel-sided or only slightly and gently tapering towards the apex which is rounded. The antero-lateral margins are slightly convex and pass into the cornua without any boundary. The cornua are very small, and shaped much as in *B. robusta* and *B. costata;* the bases of the cornua are rather broad and the distal parts project in a postero-lateral or posterior direction; these latter parts are somewhat variable in length and shape. The cornua are situated rather far backwards at the beginning of the posterior third (or thereabouts) of the median length of the main shield. The pectoral sinus are shallow and facing postero-laterally. The inter-zonal part is rather long and broad but rapidly narrowing backwards, and its posterior breadth is as great or somewhat greater than half of the maximum breadth of the shield. The inter-zonal sinus are deep and the posterior angle reaches farther backwards than the postero-lateral corners. The dorsal sensory field is narrowly oval in shape and gently tapering towards the pointed anterior end but more or less abruptly truncated at the posterior margin with rounded postero-lateral corners; the length of the field is about three times as great as the breadth. The field reaches backwards distincly behind the level of the inner end of the inter-zonal sinus. The lateral sensory fields are undivided and more or less strongly bent, forming an obtuse angle at, or somewhat anterior to, the bases of the cornua. Posteriorly they are bent down on the lateral sides of the inter-zonal part. The orbital openings are circular or roundedly oval and situated at about the same distance from the basis of the rostral process as from the posterior angle of the inter-zonal part.

The exoskeleton is in a rather imperfect state of preservation, and nothing notable has been observed about its structure.

The endoskeleton is well ossified; several of the canals for the principal superficial nerves and vessels can be seen in most of the specimens; the postbranchial wall is well displayed in nos. 154, 156, 158, 159, and partly in no. 161; parts of the shield in ventral view are exposed in nos. 156, 157, 158—161; the strongly developed neural ridge is seen in no. 157.

Remarks. — *B. puella* resembles *B. costata* and *B. robusta* (p. 476) in the feeble development of the cornua; it is most suggestive of *B. robusta* (of which it appears as a dwarf-form) but it differs from this species by the minute size, by the shape of the shield, the deeper

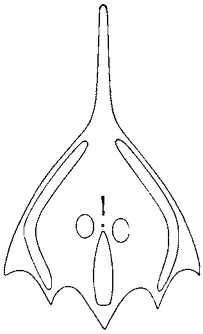

Fig. 87. — *Boreaspis puella* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (ENS no. 152) and ENS no. 158. × 2.

inter-zonal sinus, the configuration of the sensory fields, and the slightly more anterior position of the orbital openings, and it seems thus most appropriate to regard it as a species of its own.

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, the lowermost part of the C. Kjeldsen division.

Localities. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier, in red layer, about 130 m above sea-level (nos. 152—163); the two specimens, hesitatingly placed here, come from the same locality (no. 164) and from Mt Kronprinz, W. slope (no. 165).

All the specimens were collected by the ENS expedition in 1939.

3. *Boreaspis costata* n. sp.

(Fig. 88; pls. 84—85; 86:2; 87:1.)

Diagnosis. — A *Boreaspis* species of comparatively large size with maximum breadth of cephalic shield about as great as or somewhat less than length of main shield. Rostral process from about one-third to about half as long as main shield in median line, slightly increasing in breadth towards apex. Antero-lateral margins rather well curved. Cornua very small, triangular, situated rather far forward on sides of shield, projecting in postero-lateral direction. Pectoral sinus shallow, facing laterally. Inter-zonal part broad and very long; its breadth between postero-lateral angles slightly more than half as great as maximum breadth of shield. Dorsal sensory field oval, about three times as long as broad; posterior margin truncated. Lateral sensory fields undivided; gently curved at basis of cornua. Orbital openings situated distinctly behind middle of length of main shield in median line. Exoskeleton ornamented with scattered small tubercles.

Holotype. — Cephalic shield (ENS no. 168).

Material. — The material placed in this species consists of five specimens (ENS nos. 166—169 and Pal. Mus. Oslo no. D5165). Only the holotype (no. 168, pls. 85; 86:2) consists of a well preserved cephalic shield in counterpart; the others are more or less fragmentary or distorted by pressure; no. 166 (pl. 87:1) consists of the anterior part of a shield, exposed in ventral view; no. 167 (pl. 84:2) of a distorted shield in counterpart; no. 169 of an imperfect shield, partly in counterpart, and no. D5165 of the dorsal exoskeleton of a very imperfect shield, ventrally exposed. In addition to these specimens I place here with much doubt one specimen (ENS no. 170), consisting of the dorsal exoskeleton of a fragmentary shield, exposed in ventral view (pl. 84:1).

Description. — The cephalic shield of the holotype measures 40 mm from the apex of the rostral process to the posterior margin of the inter-zonal part of the ventral side; the rostral process is 15 mm long. The maximum breadth of the shield (between the tips of the cornua) is about 27 mm, and the posterior breadth of the inter-zonal part about 15 mm. In no. 169 the length of the shield (from the rostral apex to the posterior margin of the inter-zonal part on the ventral side) is 34 mm and the rostral process in only 9 mm long. The other specimens are of a similar or a slightly greater size than the holotype but on account of their imperfect state of preservation no exact measurements are obtainable. Compared with the other known species of the genus, *B. costata* was thus of large size.

The cephalic shield is flattened, and, owing to the feeble development of the cornua, rather narrow. The rostral process is long and flattened, and rather broad, its breadth being somewhat less in the basal than in the distal half; the apex is sharply rounded. The length of the process in known only in two specimens, no. 168 (the holotype) and no. 169; in the latter specimen it is much shorter than in the former (or about 3/5 of the length in this specimen). In no. 168 the rostral process is thus probably about half as long, in no. 169 probably about one-third as long as the main shield. The cornua, which are situated rather far forwards, at or slightly before the level of the orbital openings, are small and triangular, somewhat varying in shape, and directed in postero-lateral direction; the cornua thus resemble those of *B. robusta* and *B. puella*. The pectoral sinus are shallow and facing laterally. Owing to the anterior position of the cornua and of the shoulder-girdle the inter-zonal part is very long; it gradually narrows backwards; the extreme dorsal posterior end could be observed only in no. 170, doubtfully placed in this species, but is there typically developed; the posterior angle is protracted backwards for some distance but probably not very much behind the level of the postero-lateral angles. On the ventral side the inter-zonal part reaches farther backwards than on the dorsal side, and its posterior margin is somewhat emarginate medially. The shape of the dorsal sensory field is well preserved only in no. 170, doubtfully placed here, and to some extent in no. D5165; it is narrowly oval and about three times as long as broad; it tapers gently towards

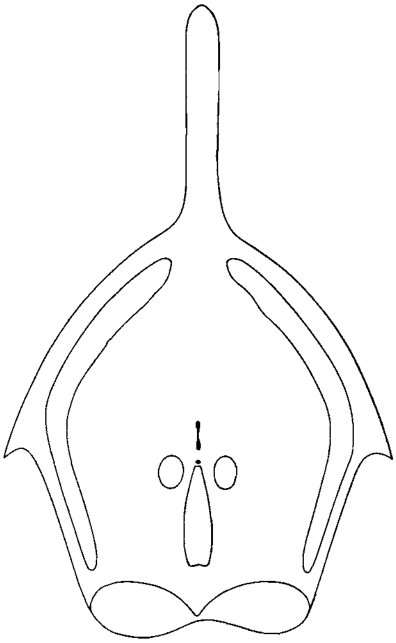

Fig. 88. — *Boreaspis costata* n. sp. Restoration of the cephalic shield in dorsal view. Mainly after the holotype (ENS no. 168). × 2.

the pointed anterior end but is abruptly truncated posteriorly. In no. D5165 it reaches backwards behind the level of the inner ends of the inter-zonal sinus, but ends before this level in no. 170. The lateral sensory fields, which are undivided, pass backwards to a point somewhat in front of the postero-lateral corners of the inter-zonal part but do not turn over to the lateral sides of this part; the fields are gently inflected at the basis of the cornua. The orbital openings, which are roundedly oval or circular in shape, lie rather far backwards, distinctly behind the middle of the length of the main shield in the median line. The pineal foramen lies between the anterior parts of the orbital openings. The posterior division of the naso-hypophyseal opening lies between the foremost parts of the orbital openings or somewhat more anteriorly.

The exoskeleton is very imperfectly preserved in most of the specimens. To judge from the conditions in the holotype the superficial layer is continuous, and its outer face is provided with scattered, small, more or less elongated, tubercles. No radiating canals are developed; on the rostral process the horizontal vascular canals are disposed in longitudinal, closely set, parallel lines.

The endoskeleton is fairly well preserved in the holotype, but also in nos. 166—167 and 169 certain structures of the endoskeleton are displayed. The inter-branchial ridges 1—4 are rather strongly developed; the three anterior ridges lie before the level of the orbits. The postbranchial wall is well shown in the holotype and in no. 167.

Remarks. — *B. costata* resembles *B. robusta* (p. 476) and *B. puella* (p. 481) in the shape of the very small cornua, and is probably closely related to these species. It is distinguished from them by the anterior position of the cornua and the consequently long inter-zonal part, and possibly also in the disposition of the inter-branchial ridges, and from these and all other species of the genus by the great size of its shield.

Geological horizons. — Upper Eodevonian (?): Wood Bay series,? the C. Kjeldsen division, the Lyktan division.

Localities. — Spitsbergen. E. side of Dickson Bay: Mt Rebbingen (= "the Mt. N. of Fiskedalen"), S. W. slope (no. 168); Mt Lyktan, the shore profile (no. D5165). W. side of Dickson Bay: Mt Borgen, N. part (no. 169). E. side of Wood Bay: Mt Scott Keltie, S. side (nos. 166—167). W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier (no. 170, doubtfully placed in this species).

No. D5165 was collected by Th. Vogt's expedition in 1925, the other specimens by the ENS expedition in 1939.

4. *Boreaspis intermedia* n.sp.

(Fig. 89; pls. 88; 89:1.)

Diagnosis. — A *Boreaspis* species of fairly large size, with maximum breadth of cephalic shield about one and a third times as great as length of main shield. Rostral process (probably) long. Antero-lateral margins slightly curved. Cornua rather short, broad at basis, rapidly tapering towards distal part, issuing from main shield somewhat behind middle of its length, projecting in lateral and somewhat posterior direction; their length constituting at most one-third of distance of their tips from basis of rostral process. Pectoral sinus broad and shallow. Inter-zonal part rather long, narrowing backwards; its posterior breadth about half as great as maximum breadth of shield. Posterior angle of inter-zonal part extending farther backwards than postero-lateral angles. Dorsal sensory field elongate, about three and a half times as long as broad; posterior margin curved. Lateral sensory fields undivided, rather strongly inflected at basis of cornua. Orbital openings comparatively large, situated distinctly behind middle of length of main shield.

Holotype. — Cephalic shield (ENS no. 171).

Material. — To this species I refer with a fair degree of certainty eight specimens, ENS nos. 171 (pl. 88:1-2), 172 (pl. 88:3-4), 173, 174 (pl. 88:5), 175 (pl. 88:6), 176—178. In addition to these, I place here with hesitation one fragmentary shield, ENS no. 179

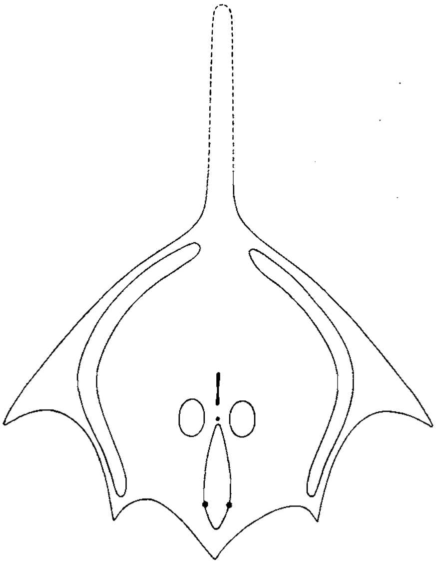

Fig. 89. — *Boreaspis intermedia* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (ENS no. 171) and ENS no. 175. × 2.

(pl. 89:1). All these specimens consist of fragments of cephalic shields, mostly in counterpart, none of them being completely preserved.

Description. — Owing to the imperfect state of preservation very few direct and exact measurements can be taken. The length of the shield from the basis of the rostral process to the posterior angle of the inter-zonal part is estimated at 20—22 mm, the maximum breadth of the shield (between the tips of the cornua) at 28—30 mm, the breadth of the inter-zonal part across the postero-lateral angles is 13—15 mm. The species is thus, compared with the other species of the genus, of fairly large size.

The rostral process is preserved with its basal part only in no. 177 and to a greater extent in no. 179, hesitatingly placed here, and therefore nothing definite can be said about its length and shape; in the last-mentioned specimen the preserved part of the process measures 9 mm, corresponding to the distance of its basis from the orbital openings. The main cephalic shield is fairly rounded and of about equal length and breadth, and the maximum breadth of the shield is about one and a third times as great as the length in the median line of the main shield. The dorsal side of the shield is slightly convex, and slopes towards the lateral margins where it passes abruptly into the horizontal cornua. The antero-lateral margins are very slightly curved, they form an angle of about 45 degrees with the main axis of the shield and pass into the cornua without any boundary. The cornua are fairly short and triangular, and project in a lateral and somewhat posterior direction. The length and shape of the cornua are somewhat varying but the basis is always broad, and they taper rapidly towards their distal parts. The cornua are situated somewhat behind the middle of the length of the main shield at about the same level as the anterior margins of the orbital openings. The pectoral sinus are broad and more or less shallow and facing postero-laterally. The inter-zonal part is long and not very rapidly decreasing in breadth backwards; its breadth between the postero-lateral angles being about one-half as great as the maximum breadth of the shield. The inter-zonal sinus are only fairly deep. The ventral portion of the inter-zonal part, which is displayed in two specimens (nos. 172, 175) only, has a deeply concave posterior margin. The dorsal sensory field is elongately oval, its maximum breadth lies at the middle, or somewhat behind the middle, of its length in the median line; the posterior margin is sharply or pointedly rounded. The field reaches rather far backwards and ends behind the level of the inner end of the inter-zonal sinus. The lateral sensory fields which are situated most laterally on the sloping part of the main shield, are undivided and rather strongly curved at the basis of the cornua; posteriorly they lie on the dorsal side and are not bent down on to the lateral side of the inter-zonal part. The orbital openings are rather large, roundedly oval, and situated rather far backwards and thus behind the middle of the length of the main shield in the median line. The pineal foramen is situated between the middle parts of the orbital openings.

The exoskeleton of the cephalic shield is too imperfectly preserved as to reveal anything of its minute structure.

Of the endoskeleton very little is to be observed in the available material.

Remarks. — With regard to the development of the cornua, *B. intermedia* takes a somewhat intermediate position between *B. costata,* (p. 483), *B. robusta,* (p. 476), and *B. puella,* (p. 481) on the one side, and the other *Boreaspis* species, particularly *B. macrorhynchus* (p. 491), and *B. batoides* (p. 489), on the other side. It is furthermore characterized by its fairly large size, the shape of the shield, and the position of the cornua. Apart from the development of the cornua, *B. intermedia* differs from *B. puella* by the greater size of its shield, the more anteriorly placed cornua, the broader shield, the shape of the inter-zonal part etc., from *B. robusta* i. a. by a somewhat larger and broader shield, more posteriorly placed orbital openings, narrow dorsal field, and from *B. costata* mainly by a somewhat smaller shield, shorter inter-zonal part, somewhat pointed posterior margin of the dorsal field; from *B. macrorhynchus* it is distinguished i. a. by the great size of its shield and the shape of the dorsal field and from *B. batoides,* which is of about equal size, mainly by the somewhat narrower shield, the shape of the inter-zonal part, and the rather large orbital openings.

Geological horizon. — Upper Eodevonian: Wood Bay series, the C. Kjeldsen division.

Localities. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier (nos. 177—178, and no. 179, hesitatingly placed here); E. side of Bock Bay: Mt Kronprinz, W. slope (nos. 171—176).

All the specimens were collected by the ENS expedition in 1939.

5. *Boreaspis batoides* n. sp.

(Fig. 90; pl. 95:1.)

Diagnosis. — A *Boreaspis* species of fairly large size with maximum breadth of cephalic shield much greater than length of main shield. Rostral process long, equalling two-thirds of length of main shield; anterior half of rostral process rather rapidly tapering towards pointed apex. Antero-lateral margins almost straight. Cornua well developed, projecting from middle of lateral sides of shield in lateral and somewhat posterior direction. Pectoral sinus broad and shallow. Inter-zonal part rather long, rapidly narrowing backwards, its posterior breadth slightly more than half as great as breadth of shield between bases of cornua. Posterior angle protracted backwards as broad median process, reaching far behind postero-lateral angles. Dorsal sensory field elongate, about three and a half times as long as broad, its posterior margin sharply curved. Lateral sensory fields undivided, strongly angulate at bases of cornua. Orbital openings small, situated distinctly behind middle of length of main shield.

Holotype. — Cephalic shield (ENS no. 180).

Material. — This species is based on a single specimen (ENS no. 180), which consists of a cephalic shield with the cornua broken off near their bases.

Description. — The dimensions of the holotype are as follows: The length of the shield in the median line between the tip of the rostral process and the posterior end of the inter-zonal part measures 31.5 mm, the rostral process is 12.5 mm long, the breadth of the inter-zonal part between its postero-lateral angles is 10 mm, and the breadth of the cephalic shield between the bases of the cornua (= between the most lateral corners of the lateral sensory fields) is about 17.5 mm. Compared with the other species of this genus *B. batoides* thus attained a fairly large size.

The shape of the main shield is roughly rhomboidal, about as broad as long, the antero-lateral margin of one side is almost parallel to the postero-lateral margin of the other side. The maximum breadth of the shield (which lay between the tips of the cornua) was certainly much greater than (more than one and a half times as great as) the length in the median line of the main shield. The rostral process is strongly

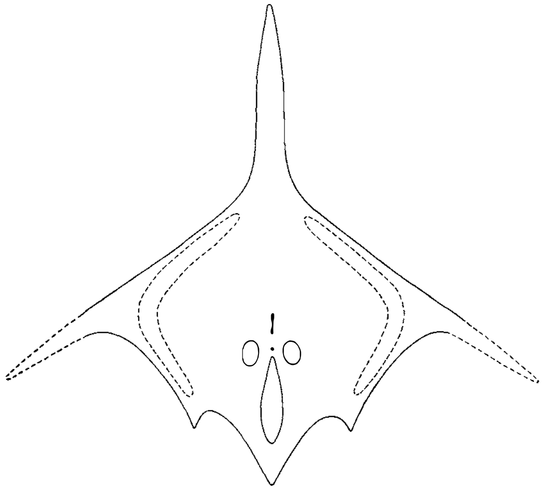

Fig. 90. — *Boreaspis batoides* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (ENS no. 180). × 2.

developed, its length constitutes about two-thirds of the length of the main shield. The lateral margins of the process are almost parallel in its basal half; in the distal half, they taper rather rapidly towards the pointed apex of the process. The antero-lateral margins of the shield are straight, and form an angle of about 50 degrees with the main axis of the shield; they pass without any boundary into those of the cornua. The cornua are preserved only in their basal parts, but seem to have been well developed and rather long, the distal portion of the preserved part pointing into a postero-lateral direction. The cornua issue from the cephalic shield at a level distinctly anterior to that of the orbital openings. The pectoral sinus are very broad and shallow. The inter-zonal part is long and rather rapidly narrowing backwards; its posterior breadth is thus comparatively small and slightly more than half as great as the breadth of the shield between the bases of the cornua. The median portion of the inter-zonal part is strongly protracted backwards, and the posterior angle reaches far behind the postero-lateral angles. The exact shape of the dorsal sensory field cannot be ascertained, but it seems to have the shape given in the restoration in fig. 90, and thus was elongate, about three and a half times as long as broad, with rounded posterior margin; the posterior end of the field lies behind the level of the inner end of the inter-zonal sinus. The shape of the lateral fields too cannot be observed directly, but to judge from the branching of the nerve canals for the fields, they are undivided and very strongly angulated at the bases of the cornua. The orbital openings are small in proportion to the size of the shield, roundedly oval, and situated distinctly behind the middle of the distance between the basis of the rostral process and the posterior end of the inter-zonal part.

At least at the margins of the rostral process and on the cornua the exoskeleton is ornamented with minute tubercles. The superficial layer is probably continuous. Nothing has been observed which can be regarded as radiating canals; along the rostral process there are, however, longitudinal, parallel vascular canals in the middle layer.

The endoskeleton is well developed and several of the superficial canals for the nerves and vessels can be seen.

Remarks. — *B. batoides* is rather suggestive of *B. macrorhynchus* but differs from this species by the large size, the general shape of the cephalic shield, the shape of the rostral process and the form of the inter-zonal part. The species is of about the same size as *B. intermedia* (p. 486) and differs from it by the longer cornua, the broader shield and the shape of the inter-zonal part.

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, the lowermost part of the C. Kjeldsen division.

Locality. — Spitsbergen. W. side of Wood Bay, Mt Sigurd, slope towards the Hoffnung-Glacier.

The single specimen was collected by the ENS expedition in 1939.

6. *Boreaspis macrorhynchus* n. sp.

(Fig. 91; pls. 92:1; 93:1; 94; 95:2.)

1927. ? *Boreaspis rostrata* in part, Stensiö, p. 295; pl. 13.

Diagnosis. — A *Boreaspis* species of rather small size, with maximum breadth of cephalic shield up to twice as great as length of main shield. Rostral process strongly developed, its length contained about one and a half times in length of main shield. Antero-lateral margins of cephalic shield straight or very slightly convex. Cornua robust, fairly long, projecting from middle of sides of shield in lateral and somewhat posterior direction; their length contained about two and a half times in distance of their tips from basis of rostral process. Pectoral sinus broad and rather shallow. Inter-zonal part rather long, somewhat narrowing backwards; its posterior breadth somewhat less than one-half of maximum breadth of shield. Posterior angle reaching backwards behind postero-lateral angles. Dorsal sensory field elongate, about three times as long as broad, abruptly truncated posteriorly. Lateral sensory fields fairly strongly inflected at bases of cornua; posterior part lying on dorso-lateral sides of inter-zonal part. Orbital openings roundedly oval, situated behind middle of length of main cephalic shield.

Holotype. — Cephalic shield (ENS no. 183).

Material. — The material, which I refer to this species with a fair degree of certainty, consists of seven specimens (ENS nos. 181—187); nos. 181 (pls. 93:1; 94:2), 182 (pl. 95:2), 183 (pls. 92:1; 94:1) representing more or less complete cephalic shields, nos. 181, 183 of them are in counterparts; nos. 184—185 consist mainly of the dorsal exoskeleton of imperfect shields, and nos. 186—187 of shields in counterparts, lacking the distal parts of the rostral process and the cornua. In addition, there is one specimen (ENS no. 188) which is placed in this species with much doubt.

Description. — The length between the apex of the rostral process and the posterior end of the shield is 22 mm in the holotype and 21.5 mm in no. 182, the rostral process is about 8.5 mm long in both specimens; the maximum breadth of the shield is about 22 mm in the holotype and about 23 mm in no. 181, in no. 185 it is estimated at about 25 mm; the posterior breadth of the inter-zonal part is 9 mm in no. 192, about 9 mm in the holotype and 9.5 in no. 182. The dimensions of no. 188, doubtfully placed in this species are as follows: the distance between the basis of the rostral process and the posterior angle amounts to about 13 mm, the maximum breadth of the cephalic shield is 18.5 and the breadth of the inter-zonal part is 9.5 mm. — The species attained thus a rather small size.

The main shield is slightly convex, while the cornua are horizontally extended. The main shield is about as long as broad but the maximum breadth of the shield is one and a half to twice as great as the length of the main shield. The rostral process is long and rather stout, it tapers more (the holotype) or less (no. 182) towards its apex, and the very apex is pointed in the holotype whereas in no. 182 it is blunt. The length of the process amounts to about two-thirds of the length of the main shield. The antero-lateral margins of the shield are almost straight, there are no distinct boundaries between the outer margins of the cornua and those of the main shield. The cornua are well developed; they are situated comparatively rather far forwards, and issue from the middle of the sides of the main shield; they are fairly robust, rather broad at their bases but rapidly narrowing towards their more or less pointed tips; the length of the cornua is contained about two and a half times in the distance of the tips from the basis of the rostral process; they project in a postero-lateral direction and are totally devoid of denticles. The pectoral sinus are rather broad and shallow. The inter-zonal part is long and broad, gently and not very much narrowing backwards; its posterior breadth is less than one-half of the maximum breadth of the shield and two-thirds of the breadth of the main shield (between the basis of the cornua). The posterior angle reaches backwards to a point somewhat behind the level of the postero-lateral angles; the inter-zonal sinus are not very deep. The dorsal sensory field is narrowly elongate; its breadth measures about one-third of its length; the posterior margin is narrow and rather abruptly truncated. No. 185 differs from the other specimens in the most posterior part of the field being rather abruptly narrowing in such a way that the field

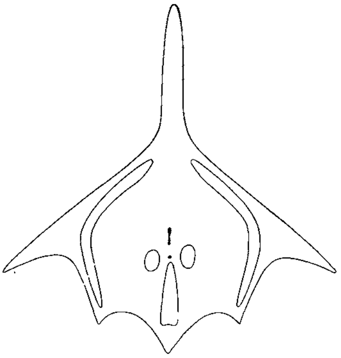

Fig. 91. — *Boreaspis macrorhynchus* n. sp. Restoration of the cephalic shield, dorsal view. Mainly after the holotype (ENS no. 183). × 2.

ends in a small median posterior process. The lateral sensory fields are narrow and undivided; they are fairly strongly inflected at the bases of the cornua; posteriorly they end on the dorso-lateral slope of the posterior portion of the inter-zonal part. The orbital openings are roundedly oval in shape and situated distinctly behind the middle of the length of the main shield. The pineal foramen lies between the middle parts of the orbits and the posterior end of the naso-hypophyseal opening at a level with the anterior margins of the orbital openings or distinctly before this level.

The exoskeleton is in most of the specimens too poorly preserved as to reveal anything of its minute structure; in the nos. 185—187 it is, however, better preserved. The superficial layer seems to be continuous and its outer face to be devoid of any kind of ornamentation. Along the lateral margins of no. 185 there are seen traces of the horizontal vascular canals in the middle layer, which here lie in parallel rows, following the margin of the shield. The mucous canals are slightly variable in calibre, and form a network which is not especially uniform or fine-meshed.

The endoskeleton is well ossified, and rather much of the internal structures is seen, especially in the nos. 181 and 182. The former (pls. 93:1, 94:2) reveals several of the structures of the ventral side of the cephalic shield, of the visceral endoskeleton, and parts of the post-branchial wall. In the latter specimen (pl. 95:2) there are i. a. exposed canals of the principal superficial nerves and vessels. In this specimen an anomaly is observed in the development of the nerve canals for the lateral sensory fields in so far that on the left side of the shield there are six independent canals of this kind, one accessory canal (sel_{2b}) being intercalated between the normal second and the third canal; on the right side of the shield the nerve canals are apparently normally developed.

Remarks. — *B. macrorhynchus* resembles rather much *B. batoides* (p. 489) but is smaller than this species, the bases of the cornua are comparatively broader, and the shape of the inter-zonal part is different. It is also somewhat suggestive of *B. circinus* (p. 504) but differs from that species i. a. by the development and the position of the cornua, and by the longer rostral process. From *B. spinicornis* (p. 497) it differs mainly by the long rostral process, by the shape of the shield and the form, position and direction of the cornua as well as by the undivided lateral fields. It reminds furthermore somewhat of *B. rostrata* but has a larger shield, shorter, more laterally directed and more anteriorly placed cornua, and the rostral process is comparatively somewhat shorter than in this species. The similarity between the two species is also illustrated by the fact that the second specimen, placed by Stensiö (1927, p. 295) in *B. rostrata,* (although too imperfectly preserved as to allow a definite specific determination to be made) probably seems to belong to *B. macrorhynchus.*

No. 188 doubtfully placed in *B. macrorhynchus* differs from the other specimens by the much slenderer cornua directed in a more postero-lateral direction and placed more backwards on the shield as well as by the broader inter-zonal part, but it cannot be decided whether it may form a different variety of *B. macrorhynchus* or belong to a species of its own.

Geological horizon. — Upper Eodevonian: Wood Bay series, the C. Kjeldsen division.

Localities. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier (nos. 181—185); Mt Kronprinz, E. slope, opposite Stjørdalen Valley (nos. 186—187). E. side of Bock Bay: Mt Kronprinz, W. slope (no. 188, doubtfully placed here).

All the specimens were collected by the ENS expedition in 1939.

7. *Boreaspis rostrata* Stensiö.

(Fig. 92; pl. 91.)

1927. *Boreaspis rostrata,* Stensiö, p. 295; fig. 78; pls. 14—15 (not pl. 13).

Diagnosis. — A *Boreaspis* species of small size with maximum breadth of cephalic shield somewhat less than length of shield in median line (incl. rostral process) and about one and a half times as great as length of main shield. Rostral process long and slender. Antero-lateral margins slightly curved, passing into those of the cornua without any boundary. Cornua well developed, slender, moderately long, issuing from main shield somewhat behind middle of its length, projecting in postero-lateral direction, not reaching as far backwards as posterior end of inter-zonal part; their length constituting about two-fifths of distance of their tips from basis of rostral process. Pectoral sinus rather broad and deep. Inter-zonal part rather broad. Posterior angle (probably) reaching backwards behind postero-lateral angles. Dorsal

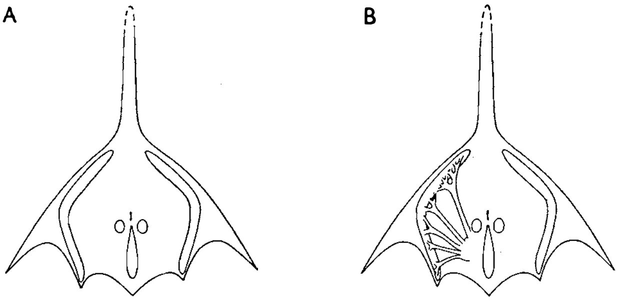

Fig. 92. — *Boreaspis rostrata* Stensiö. Restoration of the cephalic shield, in dorsal view; after the holotype (Pal. Mus. Oslo no. 96) and ENS no. 254; in B the nerve canals of the left lateral sensory field are indicated. × 2.

sensory field very narrow, about four times as long as broad, with greatest breadth in posterior half. Lateral sensory fields undivided, inflected at anterior parts of bases of cornua. Orbital openings situated at, or somewhat behind, middle of length of main shield.

Holotype. — Cephalic shield (no. 96) in the Palæontological Museum, Oslo (Stensiö 1927, p. 295).

Material. — The material of this species is very limited. I have had the opportunity to restudy the holotype (Pal. Mus. Oslo no. 96). In the new material at my disposal there is one specimen (ENS no. 254), which I refer to this species with a fair degree of certainty, and another one (ENS no. 255), which I place here with some hesitation. Both specimens consist of incomplete cephalic shields, in counterparts; no. 254 (pls. 91) is somewhat distorted and lacks the distal parts of the rostral process and the cornua, no. 255 is devoid of most of the cornua and a posterior portion of the shield.

Description. — *B. rostrata* was described in detail by Stensiö (1927, p. 295—297), and his description was based mainly on a beautifully preserved specimen, exposing many important internal characters. As many of the external features of the dorsal side of the shield were not exposed and as a specimen, evidently not belonging to the species, was included, I shall here give a new description of the external characters of the species based both on the holotype and on the new material now at hand and in comformity with the descriptions of the many new species erected within this genus. A new restoration of the cephalic shield is also given (fig. 92). Very few comparable measurements can be taken. The length of the rostral process in the holotype from the preserved anterior end (which is broken) to the anterior border of the oralo-branchial chamber is 8 mm, and in no. 255, where the process is completely preserved, it is 8.5 mm. The breadth of the inter-zonal part posteriorly is 8 mm in no. 254. The holotype and no. 254 seem to be of the same size whereas no. 255 is slightly larger. The species thus attained only a minute size, and is in this respect comparable with *B. triangularis* and *B. puella*.

The rostral process is long and slender, tapering very gently towards its apex. The very apex of the rostral process is missing in the holotype and the actual length of the process could thus not be ascertained but it seems likely that it was somewhat less than the length of the main shield. The antero-lateral margins of the shield are only slightly curved, and inclined at a rather acute angle to the main axis of the shield, much as in *B. triangularis* but the angle is more obtuse than in *B. puella*. There is no concavity at the basis of the cornua and the antero-lateral margins of the main shield pass without boundary into those of the cornua. The cornua are attached to the main shield with very broad bases and issue from it somewhat behind the middle of its length. The cornua are of a moderate length, which is contained about two and a half times in the distance of their tips from the basis of the rostral process; they are distinctly shorter than the rostral process; the cornua are almost straight and taper rapidly towards their very narrow, pointed apices; they project in a postero-lateral direction and do not reach backwards behind the level of the posterior end of the inter-zonal part. In their shape the cornua resemble somewhat those of *B. spinicornis* but are broader basally. The pectoral sinus are rather broad and deep. The dorsal portion of the inter-zonal part is not exposed in the holotype and only partly preserved in no. 255; in no. 254 it is also somewhat imperfect; so much, however, is seen that the inter-zonal part is fairly long and that its posterior angle reaches far backwards and most probably farther backwards than the postero-lateral angles. The inter-zonal sinus are rather shallow. The shape of the dorsal sensory field is seen in no. 254; it is very elongate and about four times as long as broad; it is broadest in its posterior half and somewhat narrowing backwards towards the sharply rounded posterior margin, and more so anteriorly towards the pointed anterior end. The posterior end of the field lies somewhat behind the level of the inter-zonal sinus. The lateral sensory fields are rather narrow and of almost uniform breadth; they are not subdivided, and are fairly strongly inflected at the anterior part of the bases of the cornua. As is distinctly seen in all the three specimens, the lateral sensory fields do not reach postero-laterally on to the cornua and there are quite certainly no such postero-lateral corners as indicated in the restoration given by Stensiö (1927, fig. 78A). The orbital openings are oval in shape and situated at, or somewhat behind, the middle of the length of the main shield. The pineal foramen lies at the anterior end of the dorsal sensory field between the middle parts of the orbital openings. The posterior circular division of the naso-hypophyseal opening is situated at a level with the anterior margins of the orbital openings.

The exoskeleton is not well accessible to observation; its outer face (as observed along the margins of the shield) is quite smooth without any ornamentation.

With regard to the endoskeleton it will here only be mentioned that the nerve canals for the lateral sensory fields are fairly uniformly radiating from the labyrinth cavity, the distance between the first and second canals being only slightly greater than that between the second and third canals.

Remarks. — In the general shape of the shield *B. rostrata* most closely resembles *B. spinicornis, B. triangularis* (p. 501), and *B. macrorhynchus* (p. 491). The two former species are of about the same size as *B. rostrata* and from both of them *B. rostrata* differs by the undivided lateral sensory fields, furthermore from *B. triangularis* by the shorter and straight cornua and the narrow dorsal sensory field, from *B. spinicornis* i. a. by the long rostral process and by the broader bases of the cornua. From *B. macrorhynchus* it differs mainly by the smaller size of its shield, and by the longer, slenderer cornua, placed slightly more backwards on the shield and directed in a more posterior direction.

The second specimen (no. 97) in Stensiö's original material (Stensiö 1927, p. 295) probably belongs to the new species *B. macrorhynchus,* described above (p. 494).

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, the lowermost part of the C. Kjeldsen division.

Locality. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier, in red layers about 130 m above sea-level (no. 254; and no. 255, hesitatingly placed here).

The holotype was, according to the label, found at the end of Wood Bay, according to Stensiö 1927, p. 297, "W. of the Hoffnung Glacier", that is, on the slope of Mt Sigurd towards the Hoffnung Glacier.

The two new specimens were both collected in 1939 by the ENS expedition.

8. *Boreaspis spinicornis* n. sp.

(Fig. 93; pl. 89:2-5.)

Diagnosis. — A *Boreaspis* species of small size, with maximum breadth of cephalic shield about one and a half times as great as length of main shield. Rostral process short. Antero-lateral margins curved. Cornua well developed, very slender, projecting in postero-lateral direction, reaching backwards about as far as postero-lateral angles of inter-zonal part. Length of cornua about one-third of distance of their tips from apex of rostral process. Pectoral sinus fairly narrow and deep. Inter-zonal part rather broad and of moderate length, narrowing backwards; its posterior breadth somewhat less than half as great as maximum breadth of shield. Posterior angle not very acute, reaching backwards behind postero-lateral angles. Dorsal sensory field about two and a half times as long as broad, broadest in posterior part; posterior margin obtusely rounded. Lateral sensory field on each side of shield subdivided into two divisions. Orbital openings situated slightly behind middle of length of main shield.

Holotype. — Cephalic shield (ENS no. 213).

Material. — The material referable to this species consists of forty-nine specimens (ENS nos. 195—243); the following of them are represented on the plates, nos. 210 (pl. 89:4), 211 (pl. 89:5), 213 (pl. 89:3), 230 (pl. 89:2). In addition to these specimens there are four other specimens (ENS nos. 244—247), which consist of very imperfectly preserved shields and which cannot be definitely determined as to species; they are placed here with hesitation. Most of the specimens in this species come from a single locality and are embedded in a rather coarse, micaceous, reddish sandstone; they consist mostly of rather badly preserved cephalic shields.

Description. — The dimensions of the shield are as follows: The length in the median line from the apex of the rostral process to the posterior angle of the inter-zonal part ranges from 10.7 mm (no. 224) to 15.8 mm (no. 219) and the mean is 13.8 mm (in 8 specimens). The maximum breadth, as directly measured in 6 specimens, varies from 13.7 mm (no. 196) to 17.3 mm (no. 213), with a mean of 16.2 mm. The breadth of the inter-zonal part between the postero-lateral angles ranges from 6.3 mm (no. 204) to 7.5 mm (nos. 212, 221, 229) and the mean is 7.1 mm (in 17 specimens). The length of the rostral process is about 2.3 mm (15 specimens), ranging from 1.7 mm (no. 224) to 3.3 mm (no. 213). The length of the cornua varies rather much, or from 3.5 mm in no. 196 to 6.5 mm in no. 219; the mean (of 22 measurements) is 5.4 mm.

As is seen from the measurements, the species is rather variable in the size and dimensions of its shield, but it is also evident, that these variations keep within certain limits, and that the shields all belong to a species of minute size.

The general shape of the main shield is fairly rounded with about equal length and breadth. The maximum breadth of the shield lies between the tips of the cornua and is about one and a half times as great as the length in the median line of the main shield and also somewhat more than the length of the shield inclusive of the rostral process; it is furthermore equal to or slightly greater than the distance of the tip of a cornu from the apex of the rostral process. The rostral process is very short, measuring only about one-fifth of the length of the main shield. The antero-lateral margins of the shield are more or less curved,

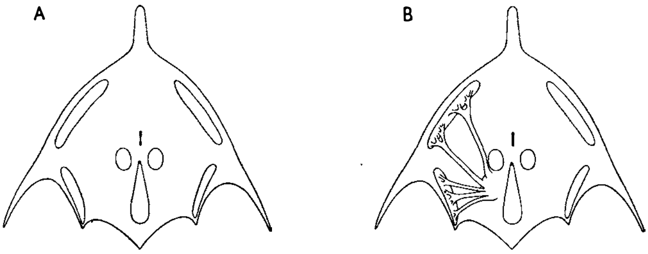

Fig. 93. — *Boreaspis spinicornis* n. sp. Restoration of the cephalic shield in dorsal view. In B the nerve canals of the lateral fields on the left side of the shield are indicated. After the holotype (ENS no. 213) and ENS nos. 262, 269. × 2.

and pass into those of the cornua without any boundary, or with a very slight concavity; in a couple of specimens (nos. 213, 221) this concavity, although slight, is nevertheless fairly distinct. The cornua are long and slender, they taper within their basal halves rather rapidly towards their distal halves which are very slender and gently narrowing towards the more or less pointed tips. The cornua issue from the main shield somewhat behind the level of the orbital openings and thus behind the middle of the length of the main shield. The cornua generally project in a postero-lateral direction, in some specimens more laterally, in others more posteriorly, and do not reach farther backwards than the posterior end of the inter-zonal part, in most specimens only as far as to the level of the postero-lateral angles. The length of the cornua is rather variable as seen from the figures given above; on the whole it is contained about three times in the distance of the tip of a cornu from the apex of the rostral process. The cornua are generally somewhat curved, in some specimens distinctly so, but in others (e. g. no. 219) they are straight and in these cases somewhat reminding of those of *B. circinus.* The pectoral sinus are ordinarily fairly narrow and deep but they vary in these respects according to the direction of the cornua. The inter-zonal part of the shield is rather broad and of moderate length and decreases more or less in breadth backwards towards the postero-lateral angles; sometimes the most posterior portion of the inter-zonal part has almost parallel lateral margins. The posterior breadth of the inter-zonal part varies from two-fifths to half the maximum breadth of the shield but is generally somewhat less than half of this breadth. The posterior angle which in most specimens is a right one or slightly obtuse, reaches backwards somewhat behind the postero-lateral angles. The inter-zonal sinus are rather shallow or fairly deep, with the deepest part usually near the latter angles. The ventral region of the inter-zonal part consists only of a narrow transverse bar and the posterior margin is only very slightly emarginate. The dorsal sensory field is elongate and about two and a half times as long as broad, its greatest breadth lying in the posterior quarter of its length; it is usually gently tapering towards the anterior end or sometimes slightly constricted in breadth in the anterior third. The posterior margin of the field generally does not reach backwards behind the level of the inner end of the inter-zonal sinus. The lateral sensory fields are subdivided into two parts on each side of the shield by a fairly narrow intervening space just inside the basis of the cornua. The anterior division of the field lies thus along the antero-lateral margin of the shield and is somewhat longer and broader than the posterior division; backwards this division reaches on to and terminates on the lateral portion of the inter-zonal part just in front of the postero-lateral angle. The orbital openings are oval in shape and situated somewhat behind the middle of the length of the main shield. The pineal foramen lies in the anterior end of the dorsal sensory field and generally between the middle parts of the orbital openings.

The exoskeleton is very badly preserved; the superficial layer seems, however, to be continuous and apparently without any kind of ornament.

The endoskeleton is well ossified but owing to the imperfect state of preservation it mostly exhibits rather little of the internal structures. The anterior division of the lateral sensory field is supplied with two nerve canals running at a rather great distance from each other; the posterior division is supplied with three nerve canals lying rather closely to each other; they are of course much shorter than those to the anterior division of the field (fig. 93B). The postbranchial wall is shown in many specimens, and stands usually almost vertically.

Remarks. — *B. spinicornis,* together with *B. triangularis* and *B. circinus* (p. 504), forms a distinct species group within the genus characterized by the constant subdivision into two parts of each of the lateral sensory fields. The species differs from them both by the short rostral process, from *B. triangularis* furthermore by the shape of the shorter cornua and the somewhat more posterior position of the orbital openings; some of the specimens of *B. spinicornis* are somewhat suggestive of *B. circinus* but the species differs from it by the smaller size of its shield, by the shape and direction of the much shorter and slenderer cornua, and by the narrower inter-zonal part. Apart from the different development of the lateral sensory fields *B. spinicornis* closely resembles *B. rostrata* (p. 494), and differs from this species mainly by the more robust shape of its shield with curved antero-lateral margins, the short rostral process, the shape and direction of the cornua, and the shape of the dorsal sensory field. It reminds furthermore of *B. curtirostris* (see this species, p. 509).

Geological horizons. — Upper Eodevonian: Wood Bay series, the upper parts of the C. Kjeldsen division, and ? the Lyktan division.

Localities. — Spitsbergen. W. side of Wood Bay: Mt Kronprinz, E. slope, opposite Stjørdalen Valley (nos. 200—204; and nos. 244—247, hesitatingly placed in this species). E. side of Dickson Bay: Mt Lyktan, S. W. slope (nos. 195—199, 241—243).

All the specimens were collected by the ENS expedition in 1939.

9. *Boreaspis triangularis* n. sp.

(Fig. 94; pl. 90:3-5.)

Diagnosis. — A *Boreaspis* species of small size with maximum breadth of cephalic shield slightly more than one and a half times as great as length of main shield. Rostral process long and slender; its length constituting about three-fifths of length of main shield. Antero-lateral margins slightly curved. Cornua well developed, long and slender, curved, issuing from main shield somewhat behind middle of its length, projecting in postero-lateral direction, reaching backwards to about same level as posterior angle of inter-zonal part; their length contained somewhat more than twice in distance of their tips from basis of rostral process. Tips of cornua with some small hooked denticles. Pectoral sinus rather deep and broad. Inter-zonal part rather narrow, posteriorly about one-third as broad as shield. Posterior angle reaching backwards behind postero-lateral angles. Dorsal sensory field about twice as long as broad, broadest in posterior part. Lateral sensory field on each side of shield consisting of two separate divisions. Orbital openings situated at or slightly behind middle of length of main shield.

Holotype. — Cephalic shield (ENS no. 251).

Material. — The material referable with a fair degree of certainty to this species consists of five specimens (ENS nos. 248—252). The holotype (no. 251, pl. 90:4) is represented by an almost entire but somewhat distorted shield in counterpart, lacking the distal part of the right cornu; the four other specimens (nos. 248, pl. 90:3; 249; 250, pl. 90:5; and 252) consist of cephalic shields, lacking parts of the cornua, no. 249 also the tip of the rostral process. There is furthermore one specimen (ENS no. 253), which because of its poor state of preservation, can be referred to this species only with some hesitation.

Description. — The length of the cephalic shield in the median line from the apex of the rostral process to the posterior end of the inter-zonal part measures 16.8 mm in the holotype and 13.8 mm in no. 250, but as the latter shield is compressed, the original length must have been somewhat greater than this figure indicates. The rostral process in nos. 248, 250, 251 and 252 measures 5, 6, 5.5 and 6.6 mm, respectively. The distance of the tip of the left cornu from the posterior angle of the inter-zonal part in the holotype is 9 mm, and the maximum breadth of the shield is thus estimated at about 18 mm. The breadth of the inter-zonal part between its postero-lateral angles measures in no. 250 6.2 mm, and in the holotype 5.8 mm. The length of the left cornu in the holotype is 6.3 mm. The species was thus only of a small size, and in this respect most closely comparable with *B. rostrata.*

In general shape the shield forms a nearly isosceles triangle, the maximum breadth being only slightly less than the distance of the tip of a cornu from the apex of the rostral process. The maximum breadth of the shield is furthermore slightly more than one and a half times as great as the length of the main shield and somewhat more than the length of the entire cephalic shield. The rostral process is apparently completely preserved in four specimens (nos. 248, 250—252); it is fairly long although the length is somewhat varying, constituting about one-third or somewhat more of the length of the whole cephalic shield. The process is slender and almost parallel-sided or very slightly broadening to somewhat behind its apex. The antero-lateral margins of the shield are slightly curved, roughly as in *B. spinicornis* and somewhat more than in *B. rostrata.* There usually is a slight concavity in the lateral margins of the shield at the basis of the cornua, and the latter are thus generally well marked off from the main shield. The cornua, which are attached to the main shield by comparatively narrow bases, are long and very slender, they are slightly curved in their entire length and somewhat more distinctly bent towards their tips; they project in a postero-lateral direction and reach backwards to about the same level as the posterior angle of the inter-zonal part. On the whole their shape is very suggestive of that of *B. gracilis.* The cornua are as long as or slightly longer than the rostral process and their length constitutes somewhat less than one-half of the distance of their tips from the basis of the rostral process. The very apex of the cornua is provided with a few small, slightly bent, hook-like denticles. The pectoral sinus are broad and rather deep, about as deep as in *B. spinicornis* and clearly deeper than in *B. rostrata.* The inter-zonal part is rather long and narrow, distinctly decreasing in breadth backwards, and its posterior breadth constitutes about one-third of the maximum breadth of the shield and about or somewhat more than half the length of the main shield. The posterior angle of the inter-zonal part reaches backwards somewhat behind the level of the postero-lateral angles, and the inter-zonal sinus are rather deep. The shape of the dorsal sensory field is inversely ovoid, thus elongate with its greatest breadth in the posterior part; the field narrows gently towards the pointed anterior end while the posterior end is obtusely rounded. The

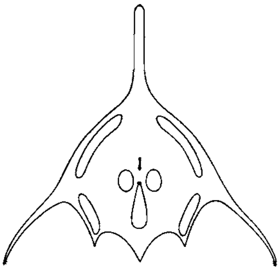

Fig. 94. — *Boreaspis triangularis* n. sp. Restoration of the cephalic shield, dorsal view. After the holotype (ENS no. 251) and ENS no. 250. × 2.

field is about twice as long as broad and is broader than in *B. rostrata* and shorter than in *B. spinicornis.* The field does not reach backwards behind the level of the inner end of the inter-zonal sinus. The lateral sensory fields are subdivided into two well separated parts on each side of the shield as is the case in *B. spinicornis* and *B. circinus.* The anterior division is situated along the antero-lateral margin of the shield and reaches backwards to about a point just anteriorly to the basis of the cornua; the posterior division, which is shorter than the anterior one, reaches from a point just posterior to the basis of the cornua along the margin of the pectoral sinus and ends on the dorso-lateral slope of the posterior portion of the inter-zonal part. Both divisions of the field are rather narrow. The orbital openings, which are comparatively large and roundedly oval, are situated at, or somewhat behind, the middle of the length of the main shield in the median line. The pineal foramen which lies in the anterior end of the dorsal sensory field is situated between the middle parts of the orbital openings. The naso-hypophyseal opening is comparatively long.

The superficial layer of the exoskeleton is continuous and smooth except towards the apex of the cornua where its face is somewhat rough, and at the very tips of the cornua which are provided with a few denticles, as mentioned before. The mucous canal system forms a network, which is rather coarse, at least in the posterior parts of the shield.

The endoskeleton is well ossified and exhibits several of its cavities and principal canals, which in general all seem to be developed as normally in the genus. From the anterior division of the lateral sensory field run two nerve canals, and from the posterior division three short nerve canals to the labyrinth cavity; they are disposed in about the same manner as in *B. spinicornis* (cf. fig. 93B).

Remarks. — *B. triangularis* comes near to *B. spinicornis* (p. 497) and *B. circinus* (p. 504) in the peculiar development of the lateral sensory fields, and is probably closely related to these species. Apart from this character, *B. triangularis* very much resembles *B. gracilis* (p. 510) in the general shape of its shield but the shield is not so broad as in this species, and differs furthermore by its much smaller size. It is of about the same size as *B. spinicornis* and *B. rostrata;* from the former species it differs mainly by the shape of its longer cornua, the long rostral process and the development of the inter-zonal part; from the second species (p. 494) it differs by the longer and more curved cornua, attached with narrower bases to the main shield, furthermore the dorsal sensory field is much broader and the lateral fields are subdivided. *B. triangularis* differs from *B. circinus* by the development of the cornua and by not inconsiderably smaller size of the shield.

Geological horizon. — Upper Eodevonian: Wood Bay series, the upper part of the C. Kjeldsen division.

Locality. — Spitsbergen. W. side of Wood Bay: Mt Kronprinz, E. slope, opposite the Stjørdalen Valley, in a grey sandstone (nos. 248—253).

All the specimens were collected during the ENS expedition in 1939.

10. *Boreaspis circinus* n. sp.

(Fig. 95; pls. 90:1-2; 92:2.)

Diagnosis. — A *Boreaspis* species of small size, with maximum breadth of cephalic shield about twice as great as length of main shield. Rostral process well developed, its length contained about twice in length of main shield. Antero-lateral margins almost straight, with a slight concavity at bases of cornua. Cornua very long and slender, issuing from main shield behind middle of its length, projecting in postero-lateral direction, reaching backwards to level with posterior angle of inter-zonal part; their length being contained about twice in distance of their tips from basis of rostral process. Pectoral sinus very broad and fairly deep. Inter-zonal part rather broad, slightly narrowing backwards, its posterior breadth slightly less than one-third of maximum breadth of shield. Inter-zonal sinus shallow. Dorsal sensory field about two and a half times as long as broad with curved posterior margin. Lateral sensory field on each side of shield subdivided into two parts. Orbital openings situated distinctly behind middle of length of main shield.

Holotype. — Cephalic shield (ENS no. 191).

Material. — To this species I refer five specimen, ENS nos. 189, 190 (pl. 90:2) 191 (pl. 90:1), 192, and 193 (pl. 92:2); they all consist of fairly complete cephalic shields in counterpart. One additional specimen (ENS no. 194) is too imperfectly preserved as to be specifically determined with any certainty; it is placed here with hesitation.

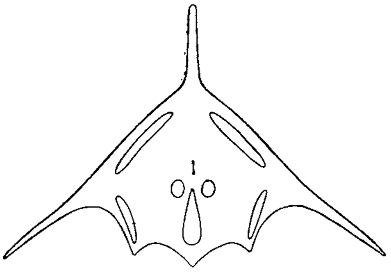

Fig. 95. — *Boreaspis circinus* n. sp. Restoration of the cephalic shield, dorsal view. Mainly after the holotype (ENS no. 191) and ENS no. 190. × 2.

Description. — The dimensions in mm of the shields are as follows (figures in brackets are approximate):

Nos.	189	190	191	192	193
Length of shield in median line	16.8	16.8	17.9	—	20
Maximum breadth	24.5	21.4	(26.5)	(24)	(28)
Breadth of inter-zonal part, posteriorly	8	7	8.4	—	9.4
Length of rostral process	5.4	5.4	5.2	—	7.5
Length of cornua	8.4	7.2	10	7.5	10

The general shape of the cephalic shield is broadly triangular. The maximum breadth (between the tips of the cornua) is about one and a half times as great as the length of the entire shield, and about twice as great as the length of the main shield in the median line. The rostral process is well developed but not very long, about half as long as the length of the main shield. The process is generally slender and of uniform breadth; in no. 193, however, it is more heavily built and tapering towards its apex. The antero-lateral margins of the shield are almost straight with a slight or very slight concavity at the bases of the cornua, thus marking off the cornua from the main shield. The cornua are very long, slender and straight; they issue from the main shield behind the middle of its length at about a level with the orbital openings, and project in a postero-lateral direction without reaching backwards behind the posterior angle of the inter-zonal part; their length constitutes about one-half of the distance of their tips from the basis of the rostral process. The pectoral sinus are broad and fairly deep. The inter-zonal part is rather long and broad, narrowing more or less rapidly backwards, and its posterior breadth is contained slightly more than three times in the maximum breadth and twice in the length of the shield in the median line. The inter-zonal sinus are distinct but not deep. The postero-dorso-median process of the inter-zonal part, which forms a right posterior angle, reaches backwards only slightly behind the postero-lateral angles. The dorsal sensory field is rather broadly elongate and about two and a half times as long as broad; its greatest breadth lies in the posterior half of the field; anteriorly the field is pointed while its posterior margin is rounded. The posterior end of the field reaches backwards to a level with the inner end of the inter-zonal sinus. The lateral sensory field on each side of the shield is subdivided into two divisions, an anterior division along the antero-lateral margin of the shield, and a posterior division, which is distinctly shorter than the anterior one, on the median zonal and the lateral inter-zonal part of the shield. The orbital openings are roundedly oval and situated distinctly behind the middle of the length of the main shield. The pineal foramen lies in the anterior end of the dorsal sensory field between the middle parts of the orbits.

The exoskeleton is badly preserved and nothing definite can be said about its structure; no ornamentation has been observed, and it seems very probable that the outer face of the superficial layer was entirely smooth.

The endoskeleton is well ossified but owing to the imperfect preservation very little can be seen of the internal structures.

Remarks. — *B. circinus* resembles *B. spinicornis* (p. 497) and *B. triangularis* (p. 501) in having the lateral sensory fields subdivided into two portions on each side of the shield. It differs from them both by the long, slender, and straight cornua, and from *B. spinicornis* furthermore by the better developed rostral process.

Geological horizon. — Upper Eodevonian: Wood Bay series, the upper part of the C. Kjeldsen series.

Localities. — Spitsbergen. E. side of Bock Bay: Mt Kronprinz, W. slope (nos. 192—193). W. side of Wood Bay: Mt Kronprinz, E. slope, opposite Stjørdalen Valley, in a red-brown sandstone (nos. 189—191; and no. 194, hesitatingly placed in this species).

All the specimens were collected by the ENS expedition in 1939.

11. *Boreaspis curtirostris* n. sp.

(Fig. 96; pls. 92:3-5; 93:2.)

Diagnosis. — A *Boreaspis* species of medium size with maximum breadth of cephalic shield from about one and a third to about one and three-fourths times as great as length of main shield. Rostral process very short, its length being contained about four times in length of main shield. Antero-lateral margins more or less curved, without or with a very slight concavity at bases of cornua. Cornua long and very slender, somewhat curved, issuing from main shield behind middle of its length, projecting in postero-lateral or posterior and somewhat lateral direction, reaching backwards to same level as posterior end of inter-zonal part; length of cornua contained somewhat more than twice in distance of their tips from basis of rostral process. Pectoral sinus comparatively narrow and deep. Inter-zonal part gently narrowing backwards, its posterior breadth being contained about twice or two

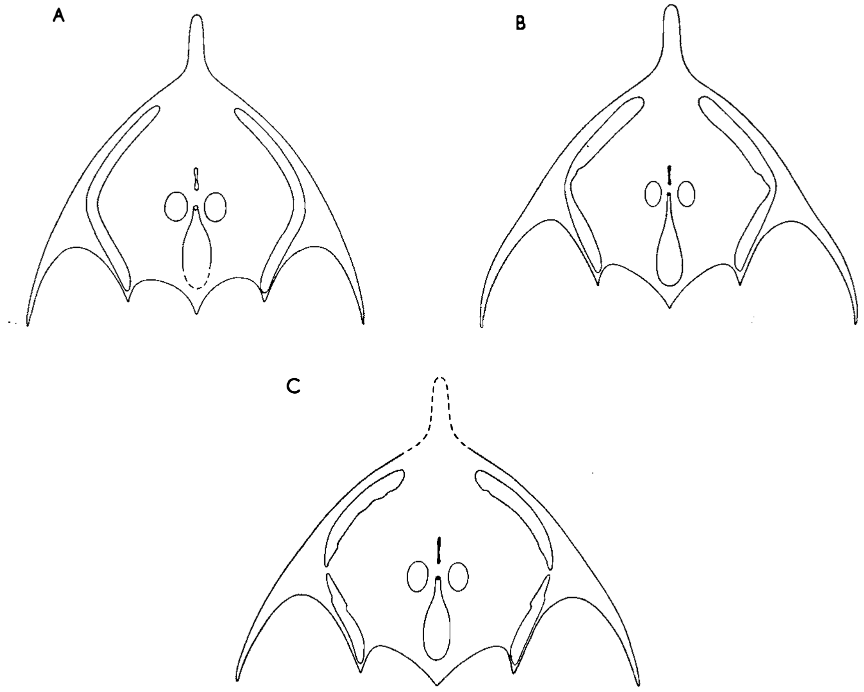

Fig. 96. — *Boreaspis curtirostris* n. sp. Restoration of cephalic shields in dorsal view, A, after ENS no. 269, B, after the holotype (ENS no. 262) and ENS no. 271 (the lateral sensory fields), C, after ENS no. 261. × 2.

and a half times in maximum breadth of shield. Posterior angle reaching backwards slightly behind postero-lateral angles. Dorsal sensory field about three times as long as broad, narrow anteriorly. Lateral sensory fields rather abruptly bent inside bases of cornua, and here sometimes constricted or (exceptionally) interrupted by a narrow gap. Orbital openings situated slightly or distinctly behind middle of length of main shield.

Holotype. — Cephalic shield (ENS no. 262).

Material. — The material referable to this species consists of twenty specimens, Pal. Mus. Oslo nos. A21614, A24875 and ENS nos. 256—260, 261 (pl. 92:3), 262 (pl. 92:5), 263—268, 269 (pl. 92:4), 270—273. In addition to these specimens I refer to the same species, though with some hesitation, two specimens, ENS nos. 274 (pl. 93:2) and 275. The specimens all consist of cephalic shields, those from Mt Triplex being badly preserved, while those from Mt Borgen, embedded in a rather coarse light grey sandstone, often well display the general shape of their shields; the inner structures, however, are very badly preserved in all these specimens.

Description. — The length of the cephalic shield from the apex of the rostral process to the posterior end of the inter-zonal part measures from 17 mm (no. 270) to 20 mm (no. 271), being 19.5 mm in the holotype; the length of the rostral process varies from 2.6 mm (nos. 270, 272) to 4 mm (nos. 259, 269) and is 3.8 mm in the holotype. The maximum breadth of the shield (between the posterior ends of the cornua) varies from 22.5 mm (nos. 266, 269) to about 26 mm (nos. 261, 271), being 22.3 mm in the holotype. The breadth of the inter-zonal part between the postero-lateral angles varies from 9 mm (the holotype and no. 270) to 11.3 mm (no. 266). The length of the cornua ranges from 7.2 mm (no. 266) to 9.5 mm (no. 261); in the holotype the cornua measure 8.2 mm and 9 mm, respectively. *B. curtirostris* is thus, compared with the other species of the genus, of medium size.

The main shield is roughly circular in general shape. The maximum breadth is somewhat variable according to the length and direction of the cornua, being in some specimens about one and a third, in others one and three-fourths times as great as the length of the main shield in the median line. The rostral process is very short but of somewhat varying length (as seen from the figures above), its length constituting only about one-fourth of the length of the main shield. The antero-lateral margins are inclined at a somewhat varying angle to the main axis of the shield; they are more or less convex and have either a rather slight concavity at the bases of the cornua or pass without interruption into those of the cornua. The cornua are long and very slender, more or less curved, and taper gently towards their tips; they issue from the main shield behind the middle of its length. The direction of the cornua is somewhat varying, they are directed postero-laterally or in a posterior and somewhat lateral direction; owing to the flexure of the cornua their distal parts are directed more posteriorly than their proximal parts. The cornua extend backwards slightly behind the posterior end of the inter-zonal part and their length, which is somewhat variable, constitutes in general slightly less than one-half of the distance of their tips from the basis of the rostral process. The pectoral sinus are rather deep and vary according to the direction of the cornua from broad to fairly narrow. The inter-zonal part is broad and fairly long, narrowing backwards, and its posterior breadth constitutes from about one-half to about two-fifths of the maximum breadth of the shield. The posterior angle is a right one or slightly acute, and extends backwards to a point slightly behind the postero-lateral angles. The inter-zonal sinus are asymmetrically developed and fairly deep. The dorsal sensory field is about three times as long as broad, its greatest breadth lies in its posterior half; the field is rather rapidly constricted in its anterior third, and this anterior part is thus very narrow; the posterior margin of the field is sharply rounded. Posteriorly the field extends distinctly behind the level of the inner ends of the inter-zonal sinus.

In most specimens it is very difficult to form a clear idea of the shape of the lateral sensory fields; in some specimens (as in no. 269) they seem to be of a rather uniform breadth throughout their length, in others (no. 271) they are distinctly constricted at the bases of the cornua while in one specimen (no. 261) the fields are subdivided into two portions by a very narrow gap between two pointed ends. The fields are rather sharply bent at the bases of the cornua; backwards they or their posterior divisions extend to the vicinity of the postero-lateral angles of the inter-zonal part and terminate on its dorso-lateral portion. The orbital openings which are roundedly oval are situated slightly or distinctly nearer to the posterior end of the shield than to the basis of the rostral process. The pineal opening lies in the anterior end of the dorsal sensory field and between the middle parts of the orbital openings.

The exoskeleton seems to be without any ornamentation except on the tips of the cornua where there are a few denticle-like tubercles just as in *B. triangularis* but not at all so large and conspicuous as in this species. The mucous canal system forms a fine-meshed network. No radiating canals have been observed, but along the lateral margins of the shield, on the rostral process and along the dorsal sensory field there are longitudinal vascular canals, disposed in parallel rows, which form a part of the horizontal vascular canal system, which otherwise is developed as a network of anastomosing canals.

The endoskeleton was evidently well ossified but is in most of the specimens very poorly preserved, and only some of the most conspicuous inner features are shown. The canals for the lateral sensory field (or fields) are disposed much as in *B. spinicornis* (e. g. in the holotype and in no. 271). The inner structures of no. 274, hesitatingly placed in this species, are partly very well exposed (pl. 93:2).

Remarks. — *B. curtirostris* differs from the other species of the genus by the general shape of its shield, the long, very slender, somewhat curved cornua, the short rostral process, and the shape of the dorsal sensory field. It is, particularly in the character of the short rostral process, suggestive of *B. spinicornis* (p. 497) but is greater than this species and has longer cornua and differently developed sensory fields. It reminds furthermore somewhat of *B. triangularis* (p. 501) but is much larger, has a shorter rostral process and a dissimilar shape of the sensory fields. It is, however, to *B. gracilis* that *B. curtirostris* is most similar and to which species it is probably most closely related. It differs from *B. gracilis* mainly by the short rostral process and the more posteriorly directed cornua, and probably in the disposition of the nerve canals for the lateral sensory fields.

Geological horizon. — Upper Eodevonian (?): Wood Bay series, the Lyktan division.

Localities. — Spitsbergen. E. side of Dickson Bay: Mt Triplex, slope towards Culm Valley (nos. 256—260; and no. 275, hesitatingly placed in this species); Mt Lyktan, W. slope (no. 272; and no. 274, hesitatingly placed here), Fiskedalen Valley (no. 273). W. side of Dickson Bay: Mt Borgen, N. part (nos. 261—271). W. side of Wijde Bay (West Fiord): Mt Errol White (= "the Mtn S. of the Valley Snegledal"; nos. A21614, A24875).

Nos. A21614 and A24875 were collected by Th. Vogt's expedition in 1928, the others by the ENS expedition in 1939.

12. *Boreaspis gracilis* n. sp.

(Fig. 97; pl. 86:1.)

Diagnosis. — A *Boreaspis* species of medium size with maximum breadth of cephalic shield about twice as great as length of main shield. Rostral process long and slender; its length contained about one and a half times in length of main shield. Antero-lateral margins sligthly curved, with a marked concavity at basis of cornua. Cornua long and very slender, with pointed tips, somewhat curved, issuing from main shield somewhat behind middle of its length, projecting in lateral and somewhat posterior direction, reaching backwards to about same level as postero-lateral angles of inter-zonal part; their length constituting about half of distance of their tips from basis of rostral process. Pectoral sinus broad. Inter-zonal part rather broad, its posterior breadth contained about three times in maximum breadth of shield; posterior angle reaching backwards well behind postero-lateral angles. Dorsal sensory field about two and a half times as long as broad, with greatest breadth posteriorly. Lateral sensory fields undivided, rather gently bent at basis of cornua, of uniform breadth.

Holotype. — Cephalic shield (no. C995) in the Swedish Museum of Natural History, Stockholm.

Material. — The material upon which this species is founded is rather scanty and on the whole very poorly preserved. Besides the holotype (Swed. Mus. N. H. Sthlm no. C995) six specimens (ENS nos. 276—281) are placed here with a reasonable degree of certainty. One specimen (ENS no. 282), represented by a very imperfectly preserved shield, is doubtfully referred to this species. All the specimens are more or less distorted. The best preserved specimens are the holotype (pl. 86:1), which consists of a cephalic shield, lacking the tip of the rostral process and the posterior dorsal portion of the inter-zonal part, no. 279, which consists of a shield devoid of the left cornu and much compressed laterally, and no. 277, a cephalic shield, which is much eroded and distorted but which anyhow fairly well shows its general shape.

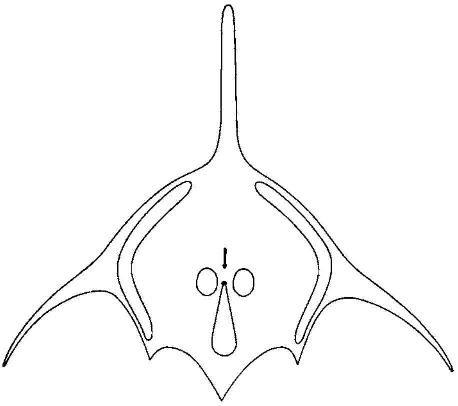

Fig. 97. — *Boreaspis gracilis* n. sp. Restoration of the cephalic shield in dorsal view. Combined after the holotype (Swed. Mus. N. H. Sthlm no C995) and ENS nos. 277, 279. × 2.

Description. — The dimensions (in mm) of the shields are shown in the following table (figures in brackets are approximate):

Nos.	C995	276	277	278	279	280
Length of main shield in median line	—	15.5	16	(15)	—	16
Length of rostral process	>6	9.5	>8	—	9.5	10.5
Maximum breadth	29.5	—	(>25)	(28)	(>24)	—
Breadth of inter-zonal part, posteriorly ..	(10)	9	8.6	—	(9.5)	10.5
Length of cornua	9 10.3	(10)	(10)	11	10	—

The species thus attained a medium size, compared with the other members of the genus.

The maximum breadth of the shield (between the tips of the cornua) is about twice as great as the length of the main shield and distinctly greater than the length of the whole shield. The rostral process is long and slender, and almost parallel-sided; its length constitutes about two-fifths of the length of the whole shield in the median line or about two-thirds of the length of the main shield. The antero-lateral margins are somewhat curved, and inclined at a more obtuse angle to the main axis of the shield than in *B. curtirostris* and *B. triangularis.* The cornua deviate rather much from the direction determined by the antero-lateral margins of the main shield and there is thus a marked concavity at their bases, much more distinct than in *B. curtirostris.* The cornua, which are attached to the main shield with a rather narrow basis, are long and very slender, gently tapering towards their pointed tips, and somewhat curved; they issue from the main shield somewhat behind the middle of its length and project in a lateral and somewhat posterior direction. The cornua reach backwards about as far as to the level of the postero-lateral angles of the inter-zonal part. The length of the cornua constitutes about one half of the distance of their tips from the basis of the rostral process and is about equal to the length of the rostral process. The cornua are very similar in shape to those of *B. triangularis* and *B. curtirostris.* The pectoral sinus are well defined, rather deep and very broad. The inter-zonal part of the shield narrows towards the postero-lateral angles, its breadth between them constituting about one-third of the maximum breadth of the shield. The posterior angle of the inter-zonal part reaches backwards far behind the postero-lateral angles; the inter-zonal sinus are comparatively shallow. The dorsal sensory field is inversely ovoid in shape, pointed towards its anterior end, bluntly rounded posteriorly, and with its greatest breadth near the posterior end; it is about two and a half times as long as broad. The field reaches backwards to about the same level as the inner end of the inter-zonal sinus. The lateral sensory fields are undivided and of almost uniform breadth throughout their length, and are rather gently inflected at the basis of the cornua; they reach backwards over the dorso-lateral sides of the inter-zonal part. The orbital openings are situated in about the middle of the length of the main shield; they are roundedly oval in shape. The pineal foramen lies in the anterior end of the dorsal sensory field and is situated between the middle parts of the orbital openings.

The exoskeleton is poorly preserved in all the specimens except in no. 276. The outer face seems to be quite smooth over the whole shield with the exception of the very tip of the rostral process where there are some few very small tubercles between the here rather wide pores of the mucous canals.

The endoskeleton is well ossified but only in no. 276 is it well preserved. The five nerve canals for the lateral sensory field are disposed in about the same way as in *B. rostrata* (cf. fig. 92B). Irrespective of the direct observation as to the shape of the lateral sensory fields it can be inferred from the ramifications of the nerve-canals within the fields that these must have been continuous and not subdivided into two parts.

Remarks. — In the general shape of its shield *B. gracilis* comes very near to *B. curtirostris* (p. 506) and *B. triangularis* (p. 501). From the latter species it is distinguished i. a. by the greater size of its shield, and above all by the continuous lateral sensory field on each side of the shield and the disposition of its nerve canals. From *B. curtirostris* it differs mainly by the longer rostral process and the more laterally directed cornua. It is, however, to this species that *B. gracilis* shows the greatest similarity, and it is very probably also most closely related to this species.

Geological horizons. — Upper Eodevonian (?): Wood Bay series, the C. Kjeldsen division, the Lyktan division.

Localities. — Spitsbergen. At Wood Bay, without indication as to the exact locality (no. C995). W. side of Wood Bay: Mt Kronprinz, E. slope, opposite Stjørdalen Valley (no. 276); Cape Roos, N. slope of the Roos Mtn (nos. 277, 278). E. side of Wood Bay: Mt Scott Keltie, S. part, W. slope (no. 279). E.side of Dickson Bay: Mt Lyktan, S. E. slope (no. 281); Mt Triplex, N. slope (no. 282, doubtfully placed here). N. of Dickson Bay: Mt Barmfjellet, Dickson Valley (no. 280).

The holotype was collected by engineer S. Lewin; the other specimens by the ENS expedition in 1939.

13. *Boreaspis ceratops* n. sp.

(Fig. 98; pl. 96.)

Diagnosis. — A *Boreaspis* species of rather large size with breadth of main cephalic shield about equalling its length. Shape of rostral process unknown. Cornua well developed (probably rather long), issuing from main shield very far anteriorly, projecting in lateral and very slightly posterior direction. Pectoral sinus very broad. Inter-zonal part very long, gently tapering backwards, its posterior breadth constituting about two-thirds of breadth of shield between bases of cornua. Posterior angle protracted backwards far behind postero-lateral angles. Dorsal sensory field somewhat more than twice as long as broad with narrow anterior part and bluntly truncated posterior margin. Lateral sensory fields partly divided into two portions by a deep notch in lateral margins inside bases of cornua. Orbital openings situated distinctly behind middle of length of main shield.

Holotype. — Cephalic shield (ENS no. 283).

Material. — This species is based on a unique specimen, (ENS no. 283); it consists of a defective cephalic shield, lacking the whole rostral process and the distal parts of the cornua.

Description. — The breadth of the shield between the bases of the cornua is about 21 mm and its length from the posterior angle to the basis of the rostral process is estimated at 22 mm or only slightly more. The breadth of the inter-zonal part between its postero-lateral angles is 14 mm. The shield is thus of a rather large size and about as large as that of *B. batoides*.

In its general shape, the main cephalic shield of *B. ceratops* forms, roughly speaking, a regular pentagon; the length and breadth are about equal, and the antero-lateral and the postero-lateral sides are of about the same length, which also is equal to the distance between the postero-lateral angles. The length and shape of the supposed rostral process is entirely unknown; its presence in the species can be inferred from the broken shape of the anterior part of the shield in the available specimen. The antero-lateral margins are very slightly curved or almost straight, they are inclined at a very obtuse angle to the main axis of the shield, more obtuse than in *B. batoides* or in any other species of the genus. A slight concavity is formed as the antero-lateral margins of the main shield pass into the anterior margins of the cornua. The cornua, which are preserved only in their basal parts, have apparently been well developed; they issue from the main shield very far anteriorly, well before the middle of the length of the main shield in the median line and far anteriorly to the level of the orbital openings. The cornua project in a lateral and slightly posterior direction and as they decrease very little in breadth in their preserved basal parts it is presumed that they actually were rather long, but their shape as presented in the restoration in fig. 98, as well as that of the rostral process, is, of course, conjectural. The cornua are much more laterally directed than in any other species in the genus but are, nevertheless, in this respect to be compared most closely with those of *B. batoides*. The pectoral sinus are broad and shallow. The inter-zonal part of the shield is very lengthened in consequence of the anteriorly situated cornua; it narrows gently and not very much backwards, its posterior breadth being contained about one and a half times in the distance between the bases of the cornua or in the length of the main shield. The posterior angle of the inter-zonal part reaches backwards far behind the postero-lateral angle, and the inter-zonal sinus are rather shallow. The dorsal sensory field is elongate and about two and a half times as long as broad, and consists of three parts: the larger middle part, which is rather long and has almost parallel lateral margins, is anteriorly rather abruptly decreasing in breadth towards the very narrow anterior part, and posteriorly, at about the level of the openings for the ductus endolymphatici, the field is likewise abruptly narrowed towards the posterior part, which forms a very short posterior process of the field; this latter part is only slightly narrower than the middle part and much broader than the anterior part, and has an abruptly truncated posterior margin. The dorsal field does not reach far backwards and not behind the level of the inner end of the inter-zonal sinus. The lateral sensory fields are rather narrow, and partly divided into two portions by a deep notch in the middle of their lateral margins. The inner margins of the fields are evenly curved without any irregularities. The anterior portion, which in its greater part lies parallel to the antero-lateral margins of the shield is posteriorly bent in a posterior direction and at the same time decreasing in breadth until it passes into the here much broader posterior portion. This portion is somewhat shorter than the anterior one, it is almost straight and lies inside the postero-lateral margins of the shield on its zonal and inter-zonal parts. It is of course impossible to say if the conditions described represent the normal ones in the species, and if other specimens had an undivided lateral field or if it was

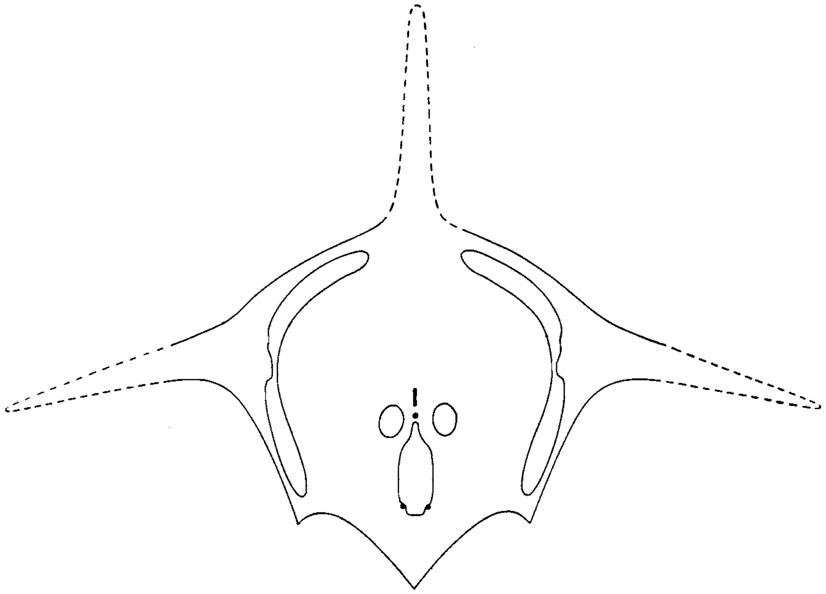

Fig. 98. — *Boreaspis ceratops* n. sp. Attempted restoration of the cephalic shield, dorsal view. After the holotype (ENS no. 283). × 2.

clearly divided into two parts (as in some other species of the genus, e. g. in *B. spinicornis).* The orbital openings, which are roundedly oval, are situated behind the middle of the length of the main shield in the median line. The pineal foramen, which lies slightly in front of the anterior point of the dorsal sensory field, is situated between the anterior parts of the orbital openings.

The exoskeleton is not easily accessible to observation but as far as can be ascertained, the outer face of its superficial layer is quite smooth without any kind of ornamentation.

The endoskeleton is well ossified. Of the five nerve canals for the lateral sensory field two enter the anterior and three the posterior portion, and the interval between the first and second canals is rather large.

Remarks. — *B. ceratops* is very imperfectly known but it is, nevertheless, well characterized by its far anteriorly situated, laterally directed cornua and the peculiar shape of the lateral sensory field (if distinguishing for the species and not only for the single specimen). Its position in the genus seems to be rather isolated and no direct and evident points of connection with the other species can be indicated. In the general shape of its shield the species resembles somewhat *B. batoides* (p. 489), and in the development of the lateral sensory field it can be compared both with *B. curtirostris* and with *B. spinicornis* and its allies.

Geological horizon. — Upper Eodevonian (Siegenian): Wood Bay series, the lowermost part of the C. Kjeldsen division.

Locality. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier, in red layers, about 130 m above sea-level.

The single specimen was collected during the ENS expedition in 1939.

Boreaspis sp.

(Fig. 99; pl. 89:6.)

The form here described is represented by a single specimen (ENS no. 284), consisting mainly of the dorsal exoskeleton of a complete cephalic shield, which is slightly distorted by pressure of the rock,

Description. — The dimensions of the shield are as follows: length in median line 15.5 mm, maximum breadth 21.5 mm, posterior breadth of inter-zonal part 7.8 mm, length of rostral process 4.3 mm, length of cornua 7 and 8.5 mm respectively. The specimen thus attained only a small size, being in this respect intermediate between *B. spinicornis* and *B. circinus*. The shield is broad, the main shield slightly broader than long, and the maximum breadth is about twice as great as the length of the main shield in the median line. The rostral process is well developed but its length is distinctly less than half of the length of the main shield, the process being thus somewhat shorter than in *B. circinus* and longer than in *B. spinicornis*. The antero-lateral margins are slightly convex. The cornua, which issue from the main shield at about the level of the orbital openings, are long and slender and slightly curved. They have a rather similar shape to those in *B. spinicornis,* tapering rather rapidly in their proximal parts while the outer parts are gently and slowly narrowing; they are, however, much longer than in *B. spinicornis*. The cornua project in a postero-lateral direction and thus more as in *B. circinus* than in *B. spinicornis*. The inter-zonal part between its postero-lateral angles is about one-third as broad as the shield between the tips of the cornua. The dorsal sensory field is rapidly decreasing in breadth in its anterior part and the anterior third of the field is thus very narrow; the field is of about the same shape as in *B. curtirostris*. It is impossible to get a clear idea of the shape of the lateral sensory fields; it could not be definitely settled whether they are subdivided into two parts on each side of the shield or not; it seems, however, possible that they have the shape indicated in the restoration, fig. 99, and that the fields on each side of the shield were interrupted by a narrow gap and thus really subdivided into two parts.

Remarks. — The specimen described above seems to represent

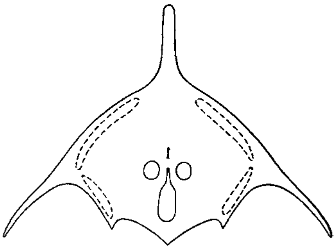

Fig. 99. — *Boreaspis* sp. Restoration of the cephalic shield of ENS no. 284, dorsal view. × 2.

a transitional form between the species *B. spinicornis* (p. 497) and *B. circinus* (p. 504). It is thus intermediate between these species in the general shape of the main shield, and in the shape of the cornua and the rostral process. It differs, however, from them both in the shape of the dorsal sensory field. As the form is in some respects imperfectly known (mainly with regard to the exact shape of the lateral sensory fields) and as it is furthermore not in any way well characterized but comes near to two closely related species we cannot describe it adequately on the basis of a single specimen but must await more and better preserved material on which this can be done, and which will allow an opinion to be formed as to its systematic rank and position.

Geological horizon. — Upper Eodevonian: Wood Bay series, the C. Kjeldsen division.

Locality. — Spitsbergen. W. side of Wood Bay: Mt Kronprinz, E. slope, opposite Stjørdalen Vallley, in a reddish sandstone. The specimen here described was collected in 1939 by the ENS expedition.

Genus **Kiaeraspis** Stensiö.

1927. *Kiaeraspis,* Stensiö, p. 297.

Diagnosis. — A cephalaspid genus with cephalic shield always longer than broad. Cornua broad and very short, issuing in lateral or in lateral and slightly posterior direction. Pectoral sinus shallow and facing postero-laterally. Inter-zonal part strongly developed, measuring at least one-third of length of shield in median line; closed ventrally with a very short ventral median, anterior process. An unpaired dorsal and one pair of lateral sensory fields (each of these latter exceptionally subdivided into two portions); posterior parts of lateral fields medially curved and continuing backwards on to interzonal part of shield. No pineal plate developed. One naso-hypophyseal opening. First nerve canal for lateral sensory field branching just medially to lateral field. Canal for r. mandibularis trigemini passing down to oralo-branchial chamber behind first nerve canal for lateral sensory field. Canal for dorso-lateral superficial vein 3 opening into canal for vena capitis lateralis closely behind orbit. Superficial layer of exoskeleton continuous; middle layer with radiating canals; mucous canal system enclosed in exoskeleton (mainly after Stensiö 1927, somewhat modified).

Type species. — *Kiaeraspis auchenaspidoides* Stensiö (1927, by monotypy).

Remarks. — The question as to the systematic position of the genus has been treated by Stensiö (1927, p. 297; 1932, pp. 151—152) and lately by Denison (1951a, pp. 192—195). In his paper of 1932 Stensiö places *Kiaeraspis* together with *Benneviaspis, Securiaspis, Hoelaspis* and *Boreaspis* in a separate genus group in his sub-family "Kiaeraspinae" on account of internal anatomical characters, thus separating it from i. a. the genera *Thyestes* and *Didymaspis* with which he had compared it previously (1927, p. 297). The first group of Stensiö, with the addition of *Cephalaspis* and several new genera, described in this paper, corresponds to the sub-family Cephalaspidinae as here defined, and it is in this sub-family of related genera we may look for the closest allies of *Kiaeraspis.* With regard to the shape of the lateral fields and their innervation *Kiaeraspis* is to be compared most closely with *Boreaspis* and *Axinaspis,* and to some extent with *Nectaspis* and *Acrotomaspis* as well as, although more remotely, with *Benneviaspis, Hoelaspis, Tegaspis* and *Ectinaspis.* In *Boreaspis* and *Axinaspis* as well as in *Kiaeraspis* the lateral fields or the posterior lateral fields are curved medially over the zonal part and extend backwards on to the inter-zonal part of the shield or even over to the dorsolateral sides of that part, and do not enter the proximal parts of the cornua. In *Nectaspis* the middle lateral field is curved in that way, and the posterior lateral field lies on the inter-zonal part; in *Acrotomaspis* the posterior lateral field lies on the inter-zonal part. In this connection we may note the fact that each of the lateral fields is subdivided into two portions in some specimens of *Kiaeraspis auchenaspidoides* and *Boreaspis curtirostris,* and constantly so in some other species of *Boreaspis* as well as in *Axinaspis whitei,* and into three portions in *Nectaspis,* and into four portions in *Acrotomaspis.* In all other genera of the subfamily the fields are constantly undivided. In *Boreaspis, (Benneviaspis* and *Hoelaspis)* the inter-zonal part of the shield has been subjected to reduction in its postero-dorsal portion as compared with that of other genera, resulting in the development of inter-zonal sinus, and also with the effect that the exoskeletal component of the inter-zonal part does not reach backwards behind the endoskeletal component, or only slightly so. This feature indicates that the mentioned genera belong to a different line of evolution than that of *Kiaeraspis.* In the development of the inter-zonal part *Kiaeraspis* approaches to some extent *Axinaspis, Acrotomaspis* and *Nectaspis.* In *Nectaspis,* however, the inter-zonal part is not strongly developed and its exoskeleton is not closed ventrally, and as the genus is differing also in other respects, e. g. by the development of the rostral parts of the shield, it is evident that the affinity between *Kiaeraspis* and *Nectaspis* cannot be very close. *Acrotomaspis* has a not very long inter-zonal part which is closed ventrally; as it differs from *Kiaeraspis* in several characters it is obvious that there is no direct relationship between this genus and *Kiaeraspis,* but it seems very probable that the two genera are in some way related, with the genus *Axinaspis* as an intermediary link. Among the genera of the sub-family Cephalaspidinae as yet known, *Kiaeraspis* seems to be most closely akin to *Axinaspis;* this genus has on the whole the same general shape of cephalic shield and thus also a comparatively long inter-zonal part. A detail in the shape of the lateral fields similarly developed in *Kiaeraspis* and *Axinaspis* may be noted here, viz. the most posterior part of the lateral field or of the posterior lateral field being markedly broadened in comparison with the anteriorly situated parts. The inter-zonal part in *Kiaeraspis* has a distinct anterior median process; a similar process is also found in *Axinaspis* and *Acrotomaspis.* The differences between *Kiaeraspis* and *Axinaspis,* besides the different length of the inter-zonal part, can in the main be ascribed to the dissimilar development of the lateral sensory fields and the ventral portion of the inter-zonal part.

Denison (1951a) is of the opinion that *Kiaeraspis* occupies an isolated systematic position ("family Kiaeraspidae") but that it may be related to "Cephalaspidae". Without entering upon his arguments it can be said that our views coincide in so far as in this paper *Kiaeraspis* (and allies) within the family is regarded as representing an evolutional line of its own.

In its geographical distribution, the genus is restricted to Spitsbergen, and stratigraphically to the upper part of the Red Bay series (Dittonian). It is as yet represented by the type species only.

Kiaeraspis auchenaspidoides Stensiö.

(Fig. 100; pl. 97:1-3.)

1927. *Kiaeraspis auchenaspidoides,* Stensiö, p. 298; fig. 79, etc.; pls. 49—58.

Diagnosis. — Same as for the genus (only species).

Holotype. — Cephalic shield (no. 98) in the Palaeontological Museum, Oslo (Stensiö 1927, p. 298).

Material. — In the material now present this species is represented by five specimens, Pal. Mus. Oslo no. A24895 (pl. 97:3), and ENS. nos. 472 (pl. 97:1), 473—474 and 475 (pl. 97:2). All the specimens consist of imperfectly or badly preserved cephalic shields.

Remarks. — As for the description of the species, the reader is referred to Stensiö (1927, p. 298; cf. also the anatomical part of his paper); through his researches *K. auchenaspidoides* appears as one of the best known cephalaspid species. Here reference will be made mainly to some points of its external morphology only, in part related to features imperfectly preserved or not shown in the original material. New restorations of the cephalic shield are also given (fig. 100).

Only the following measurements of the shields could be obtained with some reliability: the length in the median line is 16.2 mm in no. 472, and about 19 mm in no. 474; the maximum breadth is 14.3 mm in no. A24895 and about 11.7 mm in no. 472.

As is already seen from the specimens figured in the plates by Stensiö (1927, pls. 49—58) the shape of the cephalic shield is rather variable. Particularly the length of the inter-zonal part varies considerably; in the restorations (fig. 100) its extreme extent is indicated. The distance of the basis of the dorsal spine from the pineal foramen is about one and a half times (and at most twice) as great as the distance of this foramen from the rostral end of the shield. The cornua and the zonal parts are in some specimens situated somewhat more anteriorly than in others; and in consequence of this the lateral sensory fields extend backwards either over the zonal part or even as far as to the antero-dorso-lateral portions of the inter-zonal part. The cornua also vary slightly in shape, and project either in a lateral or in a lateral and somewhat posterior direction. In all specimens in the new material the rostral margin is rounded without any trace of a rostral angle, and it is very likely that this is the case in the majority of the specimens (cf. Stensiö 1927, pls. 49; 53—54; 58). The dorsal sensory field is elongate and inversely ovate in shape and thus with its maximum breadth near to the posterior margin, which is obtusely rounded; it is almost three times as long as broad. In its shape it is somewhat suggestive of that in *Hoelaspis* and in some *Boreaspis* species. Its distance from the rear end of the shield is equal to or at most twice as great as the length of the field. The lateral sensory fields are rather narrow, most anteriorly (corresponding to that part of the field which receives the branches of the first nerve canal) somewhat widened (cf. also Stensiö 1927, pl. 54:1); the posterior quarter of the field is also markedly widened (cf. Stensiö 1927, pls. 49; 53:1); the middle parts of the field are fairly narrow. In one specimen (no. 475; pl. 97:2) the lateral fields are subdivided on each side of the shield into two sections by a very narrow intervening space, the ends of the sections of the field, facing each other, being very narrow and pointed; the conditions are here very similar to those in a specimen of *Boreaspis curtirostris* (p. 506). The anterior section of the field receives the two anterior, the posterior one the three posterior nerve canals. There is no pineal plate developed.

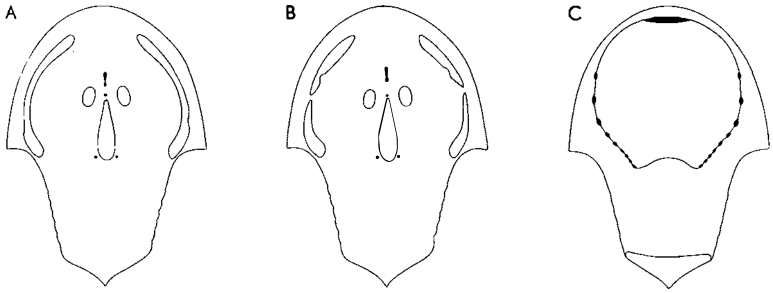

Fig. 100. — *Kiaeraspis auchenaspidoides* Stensiö. A, B, restorations of the cephalic shield in dorsal view; A, after the holotype (observe that the inter-zonal part is remarkably long in this specimen) and ENS no. 474 (the sensory fields), B, the lateral sensory fields after ENS no. 475; C, restoration of the shield in ventral view, after the holotype and Pal. Mus. Oslo no. 100. × 2.

The superficial layer of the exoskeleton is apparently continuous and probably quite smooth, at least in the main parts of the shield. In the posterior portion of the shield well developed radiating canals are observed in the middle layer. The mucous canal system is enclosed in the exoskeleton and consists very probably of a uniform fine-meshed network.

The endoskeleton is well preserved in no. A24895; some details of the lateral vascular canals are shown in pl. 97:3.

Geological horizons. — Lower Eodevonian (Dittonian): Red Bay series (the Ben Nevis division), the Ctenaspis and Benneviaspis horizons (cf. Stensiö 1927, p. 300 and Kiær & Heintz 1935, pp. 15—16).

Localities. — Spitsbergen. E.side of Red Bay: Mt Ben Nevis, W. plateau, in the Benneviaspis horizon (no. A24895), S. W. part, in talus (nos. 472—475).

No. A24895 was collected by Th. Vogt's expedition in 1928, the other specimens in 1939 by the ENS expedition.

Genus **Axinaspis** n. gen.

(ἀξινε, axe; ἀσπις, shield)

Diagnosis. — A cephalaspid genus with cephalic shield longer than broad. Rostral margin curved. Real cornua absent, represented by lateral angles on cephalic shield. Pectoral sinus absent. Inter-zonal part very long, gradually decreasing in breadth backwards, closed ventrally, provided with long ventral anterior, median process; dorsally with low median ridge. Sensory fields consisting of an unpaired dorsal field and two pairs of lateral fields; posterior part of posterior lateral field situated on inter-zonal part of shield; dorsal field elongately triangular in shape. No pineal plate. One naso-hypophyseal opening. Two nerve canals running to first lateral sensory field, three to second sensory field on each side of shield. Canal for r. mandibularis trigemini lying in visceral endoskeleton behind first nerve canal to anterior lateral sensory field. Canal for dorso-lateral superficial vein 3 opening into canal for vena capitis lateralis behind orbit. Exoskeleton with continuous superficial layer; middle layer with radiating canals. Mucous canal system enclosed in exoskeleton, forming fine-meshed network.

Type species. — *Axinaspis whitei* n. sp.

Remarks. — The genus *Axinaspis* seems to come rather close systematically to *Kiaeraspis.* Characters in common to both genera are the general shape of the shield, i. e. the feeble development of the cornua and the long inter-zonal part, the absence of a pineal plate, the disposition of the nerve canals to the lateral sensory fields, of the nerve canal V_3 and of the vein canal vls_3, and, partly, the structure of the antero-ventral portion of the inter-zonal part and of the exoskeleton; of minor importance are the somewhat similar shape of the dorsal sensory field and the most posterior part of the (posterior) lateral sensory field. The differences between the genera lie mainly in the fact that in *Axinaspis* there are two well separated pairs of lateral sensory fields while in *Kiaeraspis* the lateral sensory fields are undivided or, exceptionally, divided into two sections by a very narrow gap. Real cornua are present in *Kiaeraspis* but in comparison with these the "cornua" in *Axinaspis* are reduced merely to obtuse lateral angles on the shield.

The two genera *Axinaspis* and *Kiaeraspis* are thought to belong to an independent evolutionary line, quite different from the one represented by the genera *Benneviaspis, Hoelaspis* and *Boreaspis.* Their relation to the other genera in the subfamily is uncertain, and the two genera show no obvious resemblance, indicating possible affinity, to any of them with the conceivable exception of the genus *Nectaspis* and *Acrotomaspis.* In these genera real cornua are wanting, and the inter-zonal part is somewhat protracted backwards but not at all to the same extent as in *Axinaspis* and *Kiaeraspis.* In *Nectaspis* the elongated shape of the skield is chiefly due to the strong development of the pre-orbital part of the shield. The disposition of the principal nerve and vascular canals is in the main very similar in the three genera. *Axinaspis Kiaeraspis* and *Acrotomaspis* differ from *Nectaspis* by the inter-zonal part being closed ventrally. The fact that *Nectaspis* has three pairs and *Acrotomaspis* four pairs of lateral sensory fields is not a fundamental difference as the tendency towards a subdivision of the lateral fields appears in *Kiaeraspis,* and this subdivision occurs constantly in *Axinaspis.* It seems as if there were in some way an evolutionary connection between *Axinaspis* (and *Kiaeraspis)* and *Acrotomaspis,* yet the interrelationship between these genera and *Nectaspis* cannot be very close.

The genus *Axinaspis* contains only the type species, *A. whitei.*

The genus is only found on Spitsbergen and is here stratigraphically confined to the C. Kjeldsen division of the Wood Bay series, of which at least the lower part corresponds to the Siegenian in the European stratigraphy.

Axinaspis whitei n. sp.

(Fig. 101; pls. 97:4; 98—100; 116:2; 117:1.)

Diagnosis. — Same as for genus (only species).

Holotype. — Cephalic shield (ENS no. 466).

Material. — The material of this species consists of three specimens (ENS nos. 466—468). The holotype (no. 466, pls. 97:4; 98:1) is a fairly complete cephalic shield with fragmentary counterpart, lacking some of its central and right parts; no. 467 (pls. 98:2-3; 99; 100:2-3; 116:2; 117:1) consists of the posterior part of a cephalic shield, partly in counterpart; no. 468 (pl. 100:1) is a complete cephalic shield, rather much abraded, and distorted by pressure of the rock.

Description. — The holotype has the following dimensions: the length in the median line is 42.5 mm; the maximum breadth about 30 mm, the posterior breadth of the inter-zonal part is 14.5 mm; the distance of a lateral angle from the rostral end of the shield is 25.5 mm; the distance of the pineal foramen from the posterior and anterior ends of the shield is 23 and 19 mm, respectively. Nos. 467 and 468 are somewhat larger than the holotype, but only few exact measurements can be taken; in no. 467 the breadth of the inter-zonal part, posteriorly, is 17 mm; no. 468 is about 52 mm long.

In the general shape of its shield, *A. whitei* takes a position about midway between *Kiaeraspis* and *Nectaspis.* It is thus comparatively long and narrow owing to the strong development of the inter-zonal part, and the absence of cornua. The maximum breadth of the shield, which lies between its lateral angles is about three-fourths of the length of the shield in the median line. The rostral margin is rather strongly and evenly curved without any rostral angle. The rostral margin passes over into the lateral (or more exactly, the antero-lateral) margins of the shield without any interruption; the latter margins are slightly convex. No real cornua are developed but are represented by obtuse lateral angles about midway on the shield or somewhat nearer to the rostral than to the posterior end of the shield. The conditions are thus reminiscent of those in both *Hemicyclaspis* and *Nectaspis.* As the fins are not preserved it is of course impossible to state whether the lateral angle projected laterally to the pectoral fin or not, as in *Hemicyclaspis*. As the pectoral area, which served as a base for the pectoral fin, extends antero-laterally to a point just behind the lateral angle, it seems, however, probable that this angle did not reach far or not at all laterally to the fin but that the conditions in this respect were much as in *Hemicyclaspis*. No pectoral sinus are developed. The inter-zonal part is long and narrows only slightly backwards; its width between the postero-lateral corners being about one half as great as the maximum breadth of the shield. The inter-zonal part is closed ventrally and is here provided with an anteriorly directed, horizontal, triangular, long median process. The dorso-median and the ventro-median portions of the inter-zonal part are protracted backwards far behind its postero-lateral corners. The lateral wall of the inter-zonal part has posteriorly a deep concavity, which reaches forwards to about the middle of the length of the inter-zonal part. Dorsally in its posterior half the inter-zonal part has a rather well defined low ridge, which does not ascend in posterior direction. The dorsal portion of the inter-zonal part shows posteriorly some slight traces of transverse grooves and ridges, indicating the incorporation of trunk-segments with the cephalic shield; their exact number could, however, not be established. Of the dorsal sensory field only the posterior part is preserved in one specimen (no. 467); its transverse posterior margin is somewhat concave and its postero-lateral corners are rounded; it seems very likely that the field as a whole was rather long and triangular in shape. The openings for the ductus endolymphatici lie within the field, rather near its postero-lateral corners. The distance of the field from the posterior end of the shield is probably about twice as great as the length of the field. The anterior lateral field on each side of the shield is situated antero-laterally to the orbit near the margin of the shield at the transition between its rostral and antero-lateral margins; it is narrow and about three times as long as broad. The posterior lateral field is much better developed than the anterior one but is likewise rather narrow. Its anterior end lies about at the same level as the anterior portion of the naso-hypophyseal opening and it stretches from here in postero-lateral direction along the antero-lateral margin of the shield; at about the middle of its length the field is bent in postero-median direction forming an obtuse lateral angle, and the posterior half of the field runs parallelly to the margin of the zonal and anterior inter-zonal parts of the shield. Posteriorly the field is somewhat triangularly widened, and it ends at about the same level as the posterior margin of the dorsal sensory field. The distance between the anterior and posterior lateral sensory fields is about equal to the length of the anterior field. The orbital openings, which are comparatively small and roundedly oval, lie distinctly in front of the middle of the length of the shield and rather

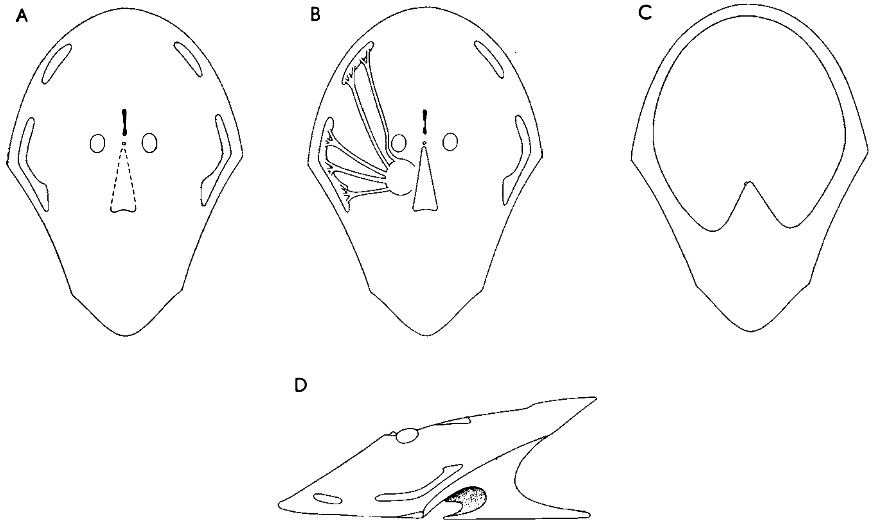

Fig. 101. — *Axinaspis whitei* n. sp. Restoration of the cephalic shield, A and B, in dorsal view (in B the nerve canals to the lateral sensory fields on the left side of the shield are indicated), C, in ventral, D, in lateral view. Mainly after the holotype (ENS no. 466) and ENS no. 467. Nat. size.

far apart, the inter-orbital breadth being about three times as great as the transverse diameter of an orbital opening. The antorbital prominence is rather strongly developed, elongate, and bordering the fossa circum-nasalis laterally. This fossa is well developed, fairly deep but not much deeper anteriorly than in its posterior part; it is broadly and roundedly triangular in shape. The naso-hypophyseal opening is of normal shape, with three rather indistinct divisions; it lies on a small median ridge in the circum-nasal fossa. The inter-orbital space is not completely preserved; it is, however, evident that there was no normal pineal plate.

The exoskeleton is well developed (pls. 116:2; 117:1). Its outer face is ornamented with rather small, not very numerous or closely set, blunt tubercles. The superficial layer is continuous and covers the middle layer; it is most strongly developed in the tubercles. The radiating canals are well developed; the vascular areas are, however, very irregular both in shape and size; one large vascular area has its centre on the antorbital prominence, another much larger area lies just postero-laterally to the dorsal sensory field. The basal layer is well developed and rather thick only in the posterior part of the shield, where the exoskeleton does not rest on the endoskeleton; no ringsinus have been observed. The mucous canal system is enclosed in the exoskeleton and, as far as could be ascertained, consists all over the shield of a uniformly fine-meshed network of rather fine canals. Nothing is known of the sensory line system.

The endoskeleton is well ossified; in the holotype it is, however, partly destroyed. The postbranchial wall is displayed in no. 467 and parts of the linings of the oralo-branchial chamber are seen in the holotype and no. 468. The canals of the superficial vessels and nerves are either not well preserved or else not easily observable owing to the strong development of the subcutaneous vascular plexus. The anterior lateral field is supplied with two nerve canals *(*sel_1—sel_2*),* the posterior one with three canals *(*sel_3—sel_5*);* the canal V_3 runs in the visceral endoskeleton behind the canal sel_1 (as e. g. in *Kiaeraspis* and *Nectaspis),* and the canal vls_3 is disposed in such a way that it must have opened into the canal *vcl* behind the orbit.

Remarks. — This remarkable species is named in honour of Dr. I. E. White of the British Museum of Natural History, London, the eminent authority on fossil fishes, who was a member and one of the leaders of the ENS expedition to Spitsbergen in 1939.

Geological horizon. — Upper Eodevonian: Wood Bay series, the C. Kjeldsen division.

Localities. — Spitsbergen. W. side of Wood Bay: Mt Sigurd, slope towards the Hoffnung Glacier, in red layers about 130 m above sea-level (nos. 466 and 467, in the same piece of rock). E. side of Bock Bay: Mt Kronprinz, W. slope (no. 468).

All the three specimens were collected by the ENS expedition in 1939.

Genus **Acrotomaspis** n. gen.

(ἀκροτομειν, to cut off at end; ἀσπις, shield.)

Diagnosis. — A cephalaspid genus with cephalic shield about as long as broad or somewhat elongate. Anterior end of shield more or less abruptly truncated or emarginate. Real cornua absent, replaced by obtuse lateral angles. Pectoral sinus not developed. Inter-zonal part rather long; lateral sides narrow; closed ventrally with anterior and posterior median processes; postero-dorso-median portion not much protracted backwards. Sensory fields small or very small, consisting of one unpaired, triangularly shaped, dorsal field and four pairs of lateral fields, three of them situated along antero-lateral margins of shield, one along postero-lateral margins of shield or near postero-lateral angle of inter-zonal part. No pineal plate. One naso-hypophyseal opening. One nerve canal entering each of the three anterior lateral fields, two the posterior lateral field. Canal for r. mandibularis trigemini in its course through visceral endoskeleton lying behind nerve canal of first lateral field, entering oralo-branchial chamber just antero-laterally to its most distal part. Canal for n. facialis running behind nerve canal to second lateral field. Canal for dorso-lateral superficial vein 3 opening into canal for vena capitis lateralis behind orbit. Superficial layer of exoskeleton generally continuous, ornamented with tubercles. Middle layer with radiating vascular canals. Mucous canal system generally enclosed in exoskeleton, consisting of uniform plexus.

Type species. — *Acrotomaspis instabilis* n. sp.

Remarks. — In this very peculiar genus a further stage in the subdivision of the lateral sensory fields seems to have been reached, as compared with normal cephalaspid genera (with only one pair of lateral fields), and with *Axinaspis* and *Nectaspis.* At first glance the genus recalls somewhat *Nectaspis* in the advanced subdivision of the lateral fields and in the non-development of the cornua, but at closer inspection we find that the differences between the two genera are fairly striking. With regard to the sensory fields the dorsal field in *Acrotomaspis* is seen to be triangular in shape with concave lateral and posterior margins, and it thus reminds somewhat of the dorsal field in *Nectaspis areolata.* The form and disposition as well as the innervation of the lateral fields (disregarding their number) is quite dissimilar in *Acrotomaspis* and *Nectaspis.* In *Acrotomaspis* the lateral fields are small or very small; the three anterior pairs are situated along the antero-lateral margins of the shield, the posterior one does not reach backwards behind the level of the orbital openings or the lateral angles of the shield. The posterior pair is situated along the postero-lateral sides of the shield; the posterior field is comparatively long in *A. instabilis* but in *A. trinodis* and in *A.* sp. 2 it is very small and located near the postero-lateral angle of the inter-zonal part. In the geologically younger forms the posterior lateral sensory field is thus much reduced compared with the older forms. All the lateral fields are elongate and straight, there is thus no field which corresponds to the angulated middle field situated inside the lateral angles of the shield in *Nectaspis.* While the nerve canals for the lateral sensory fields in *Nectaspis* are disposed in such a way that two canals run to the first field, two to the second, and one to the third, their disposition in *Acrotomaspis* is such, that the three anterior lateral fields receive one canal each, and the posterior field two canals. These differences indicate that the conditions in *Acrotomaspis* cannot have arisen from those in *Nectaspis* but that the subdivision of the lateral fields in the two genera has originated from a more primitive stage along different lines, and that the two genera cannot stand in direct genetic relation to each other.

In *Axinaspis* there are two lateral sensory fields on each side of the shield, the anterior one being supplied with two nerve canals, the posterior one, which is angularly bent inside the lateral angle of the shield and with a small portion of the field lying before this angle, receiving three nerve canals. It seems possible to regard these conditions as ancestral to those in *Acrotomaspis,* if the anterior field in *Axinaspis* is thought to be subdivided into two parts, each with its nerve canal, and an anterior portion of the posterior field, anteriorly to the lateral angle of the shield (together with one nerve canal), to be disconnected from the posterior part of the field by an interruption just inside the lateral angles. In such a way we may arrive at the conditions of the lateral fields found in *Acrotomaspis.*

The disposition of the nerve canal of the foremost lateral sensory field *(sel_1)* and its relation to the canal V_3 in *Acrotomaspis* is much the same as that of the canal sel_1 in *Kiaeraspis, Axinaspis* and *Nectaspis* as well as in *Boreaspis* and its allies. The development of the inter-zonal part of the shield and the structure of the exoskeleton preclude the assumption of a closer relationship between *Acrotomaspis* and the latter; the genus belongs to quite another line of evolution within the subfamily than *Boreaspis.*

In *Acrotomaspis* the shield is anteriorly truncated or emarginated and the rostral part of the shield is not at all lengthened (as in *Nectaspis)* although the buccal cavity is fairly well developed. The extreme rostral margin of the shield is somewhat bent down as a narrow, antero-ventrally directed border, while the antero-lateral corners of the shield are much deeper and stand vertically (see fig. 102); when viewed from in front, the shield has thus most anteriorly a broad and low ventral emargination. Possibly this indicates that the mouth was subterminal. In geologically younger forms of the genus (e. g. *A. trinodis)* the antero-lateral corners of the shield are much protracted forwards, forming acutely projecting antero-lateral angles, the rostral margin between them being rather deeply concave with a short median process.

The inter-zonal part of the shield is fairly long, longer than in *Nectaspis* but shorter than in *Axinaspis* and *Kiaeraspis.* Its lateral sides are very narrow, forming a pair of bars joining the ventral portion of the inter-zonal part, which has the shape of an elongate plate. The inter-zonal part is thus closed ventrally, contrary to what is the case in *Nectaspis;* it reminds in fact in the shape of its ventral portion of that of *Axinaspis,* being, however, much reduced in comparison with it.

The structure of the exoskeleton is very similar in *Acrotomaspis instabilis* and *Axinaspis whitei.*

We thus find it very probable that the genus *Acrotomaspis* is in some way, and possibly directly, related to *Axinaspis* and more distantly to *Kiaeraspis;* its relationship to *Nectaspis* is certainly not very close.

The genus *Acrotomaspis* contains two species, named and described below, viz. *A. instabilis* and *A. trinodis.* Besides these there exist two additional forms, *A.* sp. 1 and *A.* sp. 2, which are represented by very imperfectly preserved specimens and which therefore cannot be adequately described; they are left unnamed but very probably constitute species of their own.

With our present knowledge, the genus is restricted to Spitsbergen where it is found in the Wood Bay and in the Grey Hoek series (in age ranging from upper Eodevonian, possibly Siegenian, to uppermost Eodevonian or lower Mesodevonian).

1. *Acrotomaspis instabilis* n. sp.

(Fig. 102; pls. 101—103; 104:1-2; 118:1-2.)

Diagonsis. — An *Acrotomaspis* species of minute size with rostral margin of cephalic shield more or less abruptly truncated, antero-lateral corners not protracted. Cornual angles situated at about same level as orbital openings. Inter-zonal part distinctly narrowing backwards. Posterior lateral sensory field rather long. Distance of orbital openings from posterior end of shield about one and a half times as great as their distance from rostral margin. Outer face of exoskeleton on entire cephalic shield with very large tubercles.

Holotype. — Cephalic shield (ENS no. 450).

Material. — The material of this species consists of sixteen specimens, ENS nos. 449 (pl. 102:3), 450 (the holotype, pls. 101; 102:2), 451 (pl. 102:1), 452 (pl. 104:1-2), 453 (pl. 103:1), 454 (pl. 103:4), 455 (pl. 103:2), 456 (pl. 103:3), 457—464. With the exception of the holotype (no. 450) which is a fairly well and completely preserved shield the specimens consist all of more or less fragmentary shields or else of shields which are distorted by pressure of the rock.

Description. — Owing to the fragmentary or distorted state of the shields only few measurements can be taken. The holotype measures 12.4 mm in median length and about 11 mm in maximum breadth. No. 449 is 14 mm, no. 451 12 mm and no. 454 11.5 mm long. The height of the shield is rather considerable, being 6.7 mm in no. 452, and about 6 mm in no. 457. All the other specimens seem to be of about the same size and it is evident that the species attained only a very small size; it is, in fact, the smallest Cephalaspid hitherto known.

Taken as a whole the cephalic shield seems to be only very slightly longer than broad. The maximum breadth of the shield (between the lateral angles) lies slightly or distinctly before the middle of the length of the shield in the median line. The rostral margin of the shield is more or less abruptly truncated, the antero-lateral corners of the shield are obtuse and not protracted forwards. A very narrow strip of the rostral margin is bent down antero-ventrally. The antero-lateral margins of the shield are very slightly curved, the almost vertical antero-lateral walls of the shield are fairly high but abruptly decreasing in height on their forward passage into the rostral margin; when viewed from in front the shield has thus a broad ventral emargination (pl. 102:3). The lateral angles are placed at about the same transverse level as the orbital openings and evidently never far behind that level, thus situated before the middle of the length of the shield in the median line; their distance from the posterior end of the shield being greater than that from the rostral end. No pectoral sinus are developed, the postero-lateral margins of the shield being almost straight. The vertical postero-lateral walls of the shield are slightly concave or grooved anteriorly towards the lateral angles. The inter-zonal part is rather long but somewhat varying in length in the different specimens, being thus comparatively short in the holotype and no. 451, but comparatively long in no. 449 and no. 452; its posterior breadth is about half as great as the maximum breadth of the shield; it is distinctly narrowing backwards. The dorso-postero-median portion is protracted somewhat backwards, and thus the posterior angle reaches farther backwards than the postero-lateral angles; these latter angles are obtuse and often rounded and not well defined. When seen sideways the lateral walls of the inter-zonal part are deeply cut out in front and from behind, the lateral walls being very narrow in their ventral parts (pl. 104:1). The ventral portion of the inter-zonal part has the shape of an elongate plate with concave anterior and rounded posterior margin, the posterior end of the ventral portion reaching backwards as far as (no. 452) or farther backwards (no. 457) than the posterior end of the dorsal portion of the inter-zonal part. The maximum height of the shield is rather great, being probably about half as great as the length of the shield in the median line. In some of the specimens (nos. 449, 452, 463) the dorsal portion of the inter-zonal part shows posteriorly on each side a fairly distinct transverse groove. The inter-zonal part has most posteriorly a short, low, usually very indistinct dorsal median ridge, which, at least in no. 449, is somewhat higher posteriorly, forming a very short, postero-dorsally directed spine. The dorsal sensory field is rather variable in shape; it is always triangular with concave lateral and posterior margins, the anterior part of the field is rather or very narrow; in some specimens (e. g. no. 454, pl. 103:4) the field can be said to be three-rayed, with one long and narrow anterior, and two shorter, postero-lateral branches, often of somewhat unequal length. The distance of the field from the posterior end of the shield is somewhat or distinctly greater than the length of the field. On each side of the shield there are four lateral sensory fields, three lying along the antero-lateral margin of the shield, and one along the postero-lateral margin. The three anterior fields are very small and narrow. The most anterior field is distinctly longer than each of the others, it is

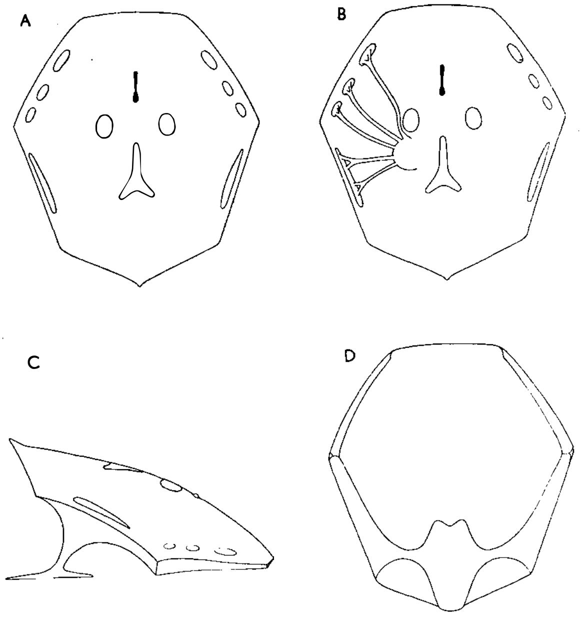

Fig. 102. — *Acrotomaspis instabilis* n. sp. Restorations of the cephalic shield, A, B, in dorsal view, in B the nerve canals for the lateral fields on the left side of the shield are indicated; C, in lateral view; D, attempted restoration of the shield in ventral view. A and B mainly after the holotype (ENS no. 450), C and D after the holotype and ENS nos. 449, 452, 457. About × 3.

somewhat variable in size, being about three or four times as long as broad. The following two fields are short, and of about equal length; they are at most twice as long as broad; the third field from in front lies somewhat before the lateral angle of the shield and never reaches backwards behind this angle. The intervals between the three anterior fields are rather small but always distinct and about as great as the length of the smaller fields. The posterior lateral field is rather long; it ends posteriorly well before the postero-lateral angle of the interzonal part; the field is always very narrow, of greatly variable length but in all specimens (where it is observed) several times as long as broad; it is straight and of rather uniform width or in some specimens somewhat broader posteriorly. The orbital openings are roundedly oval in shape and situated distinctly in front of the middle of the length of the shield in the median line. The inter-orbital breadth is about twice or slightly more than twice as great as the transverse diameter of an orbital opening. The naso-hypophyseal opening is very large; its posterior end lies generally on a level with the anterior margins of the orbital openings, or in front of this level, and from hence the opening reaches forwards, sometimes as far as to the middle of the distance between the rostral end and the orbital openings. The circumnasal fossa is very large, triangular in shape, and well defined in its anterior and middle parts. The pineal foramen in the exoskeleton, which is very small and easily overlooked, is not located in an independent pineal plate; it is situated somewhat in front of the dorsal sensory field, between the middle parts of the orbital openings.

The outer face of the exoskeleton is ornamented with very large tubercles of varying shape, some being short and blunt, others, and apparently the majority, long and acuminated; most of the latter are straightly erect, while others are more or less bent much as the medium-sized tubercles in *Thyestes verrucosus;* they are formed mainly by the middle layer of the exoskeleton. The superficial layer is in some places continuous, in other places it seems to be absent in the inter-tubercular spaces. The radiating canals in the middle layer are well developed, forming well defined vascular areas. These areas are very variable in size, in no. 451, laterally to the orbits, they are about 0.4 mm in diameter but in the posterior part of the shield there are some large vascular areas, one unpaired area (1.5 mm in diameter) with the centre somewhat before the posterior angle, and a pair of still larger areas with their centres postero-laterally to the dorsal sensory field. In the middle layer of the tubercles we find wide sinus-like vascular canals (pl. 118:2-3). The basal layer is well developed in the posterior part of the shield where it is not underlain by the endoskeleton. The mucous canal system forms closed canals in the exoskeleton or more or less open grooves; it consists of a uniformly rather fine-meshed network.

The endoskeleton is strongly ossified. The subcutaneous vascular plexus is well developed and renders the observation of the courses of many of the superficial canals rather difficult. The nerve canals for the lateral sensory fields are disposed in such a way that each of the three anterior fields receives one canal and the posterior field two canals. The canal V_3 enters the oralo-branchial chambers very far antero-ventro-laterally and, just antero-ventrally of the distal part of the canal sel_1 and just after passing through the velar ridge. The canal *VII* runs behind the canal sel_2. The canal vls_3 is observed in no. 458 and no. 461, it enters the canal *vcl* at a point some distance behind the orbit.

Remarks. — *A. instabilis* seems to be a rather variable species with regard to the length of the inter-zonal part and the more or less anterior position of the lateral angles of the shield; other possible variations in the shape of the shield are obscured by the fact that most of the specimens are distorted to a varying degree by pressure of the rock. The species is, however, distinguished by its small size, the truncated rostral margin of the shield, its obtuse and not protracted antero-lateral corners, the rather long posterior sensory fields and the large naso-hypophyseal opening.

Geological horizon. — Upper Eodevonian: Wood Bay series, the upper part of the C. Kjeldsen division.

Locality. — Spitsbergen. W. side of Wood Bay: Mt Kronprinz, E. slope, opposite Stjørdalen Valley, in a grey sandstone.

All specimens were collected here in 1939 by the ENS expedition.

Acrotomaspis sp. 1.

(Pl. 104:3.)

This form is represented by a badly preserved cephalic shield (ENS no. 465). The length of the shield is 14 mm and the maximum breadth about 12 mm. The rostral margin of the shield is somewhat emarginated, the rounded antero-lateral corners being somewhat protracted forwards but not nearly so much as in *A. trinodis.* The lateral angles are situated about as in *A. instabilis,* thus before the middle of the length of the shield and at a level with the orbital openings. The inter-zonal part narrows only slightly backwards and its dorso-posterior end is slightly protracted backwards behind the postero-lateral angles. The orbital openings are situated before the middle of the length of the shield. The naso-hypophyseal opening is not as large as in *A. instabilis;* the circum-nasal fossa is rather deep and well defined. With regard to the general shape of the shield and to the configuration of its anterior end, this form takes an intermediate position between *A. instabilis* and *A. trinodis.* Otherwise it is so imperfectly known that it seems best to leave it unnamed and without diagnosis in expectation of better preserved material; it seems, however, most probable that it represents a species of its own.

Geological horizon. — Upper Eodevonian (?): Wood Bay series, the Lyktan division.

Locality. — Spitsbergen. W. side of Dickson Bay: Mt Borgen, N. part.

The single specimen was collected by the ENS expedition in 1939.

2. *Acrotomaspis trinodis* n. sp.

(Fig. 103; pl. 105.)

Diagnosis. — A fairly small *Acrotomaspis* species with rostral margin of shield deeply emarginate, antero-lateral corners much protracted forwards, appearing as acute angles (when viewed from above), median part of rostral margin somewhat projecting forwards as short median lobe. Lateral angles of shield situated distinctly behind level of orbital openings. Inter-zonal part rather slightly narrowing backwards. Posterior lateral sensory field small, situated near postero-lateral angle of inter-zonal part. Distance of orbital opening from posterior end of shield about twice as great as their distance from rostral margin. At least antero-lateral corners and median rostral lobe with rather large tubercles, posterior part of shield with minute tubercles.

Holotype. — Cephalic shield (ENS no. 434).

Material. — To this species are referred eleven specimens (ENS nos. 434—443, 616). The holotype (no. 434, pl. 105:3), consists of the dorsal exoskeleton of a complete cephalic shield, which is somewhat flattened but otherwise not distorted, nos. 435, and 436 (pl. 105:1) consist likewise of the dorsal exoskeleton of complete shields but are somewhat distorted; no. 437 (pl. 105:4) is an almost complete shield in counterpart, distorted by pressure of the rock; no. 439 (pl. 105:2) consists of an incomplete shield which is distorted but apparently not much flattened. The other specimens consist of imperfectly preserved or much distorted shields; no. 616 shows a considerable portion of the lateral wall of the inter-zonal part and of the postbranchial wall. In addition to these specimens I place here with hesitation four specimens (ENS nos. 444—447), consisting of very badly preserved cephalic shields.

Description. — In the holotype the length of the cephalic shield in the median line from the apex of the median rostral process to the posterior end of the shield is 19.5 mm, and the maximum breadth of the shield is estimated at about 19 mm. As the other shields are incomplete or else distorted by pressure in the rock no reliable measurements can be obtained on them, but they all seem to be of about the same size as the holotype or slightly larger; the shields hesitatingly placed here (nos. 444—447) are somewhat smaller than the holotype. The species was thus distinctly larger than *A. instabilis*.

The cephalic shield is somewhat longer than broad with the maximum breadth lying near the middle of its length. The rostral margin is rather deeply concave, and this rostral emargination is bisinuate in consequence of the very median part of the margin being somewhat protracted, thus forming a short blunt median lobe. The extreme rostral margin forms a narrow border which, together with the median lobe, is directed antero-ventrally, just as in *A. instabilis* The antero-lateral corners of the shield are rather acute-angled when viewed from above owing to the fact that they form the anterior end of the antero-lateral wall of the shield which stands almost vertically; in side-view the antero-lateral corners are bluntly rounded. When the shield is flattened the corners are spread out in the horizontal plane and appear blunt-ended. and thus present a different appearance from those in the normal shield. The antero-lateral margins of the shield are somewhat curved. The lateral angles are situated about midway on the lateral margins of the shield; they are placed distinctly behind the level of the orbital openings; they are very obtuse and rounded. The postero-lateral margins of the shield are almost straight. The inter-zonal part, which is rather long, narrows only slightly backwards, and its width between the postero-lateral angles is distinctly larger than half of the maximum

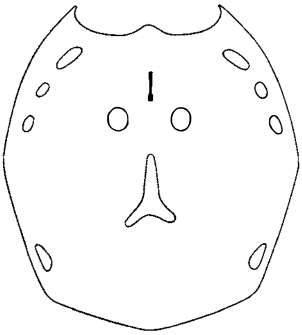

Fig. 103. — *Acrotomaspis trinodis* n. sp. Restoration of the cephalic shield in dorsal view. After the holotype (ENS no. 434) and ENS nos. 437—439. × 2.

breadth of the shield. The postero-lateral angles, as well as the posterior angle, are obtuse and rounded; the latter angle reaches backwards only slightly behind the former angles. The dorsal sensory field is varying in size and always triangular in shape with distinctly concave lateral and posterior margins. The anterior end of the field lies rather far behind the level of the posterior margins of the orbital openings. The distance of the field from the posterior end of the shield is in general about one and a half times as great as the length of the field. The lateral sensory fields are very small and narrow. The first lateral field is the longest and about or somewhat more than twice as long as broad, lying rather obliquely to the longitudinal axis of the shield inside the antero-lateral corners of the shield. The second and third lateral fields are not much longer than broad; the third field lies somewhat in front of the lateral angle of the shield. The fourth lateral field lies very far behind the three anterior ones and near the postero-lateral angle of the inter-zonal part; it is small and probably not larger than the foremost field, being thus considerably smaller than the corresponding field in *A. instabilis*. The orbital openings are roundedly oval in shape and situated rather far forwards on the shield, their distance from the apex of the median rostral lobe being about half of their distance from the posterior end of the shield. The inter-orbital breadth is somewhat more than twice as great as the transverse diameter of an orbital opening. The naso-hypophyseal opening is somewhat variable in size but comparatively smaller than that in *A. instabilis;* in most of the specimens it is rather narrow and somewhat slit-like, its three divisions being rather indistinct; it lies on a small ridge in the circum-nasal fossa. The posterior end of the opening lies distinctly in front of the level of the anterior margins of the orbital openings, and the distance between its anterior end and the basis of the median rostral lobe is about as great as the length of the opening. The circum-nasal fossa is fairly distinct but not very deep. A pineal foramen in the exoskeleton is not observed.

The exoskeleton is very imperfectly preserved, and it could not be settled whether the superficial layer is continuous or not. At least on the median rostral lobe and on the antero-lateral corners of the shield the outer face of the exoskeleton is ornamented with fairly large tubercles which are of variable shape, some being wide and blunt, others narrow and pointed; the tubercles are comparatively smaller than those in *A. instabilis*. The posterior part of the shield is ornamented with numerous very small, often stelliform (that is, with very small radiating ridges or processes) tubercles of varying shape, some rounded, others more lengthened. The middle layer is provided with well developed radiating canals, forming vascular areas of different sizes.

Very little is visible of the endoskeleton; in no. 437, however, some faint traces of the nerve canals to the lateral sensory fields are seen. In the same specimen and in no. 439 there are traces of the velar ridge, running from the vicinity of the anterior end of the naso-hypophyseal opening towards the antero-lateral corners of the shield.

Remarks. — This species, *A. trinodis,* differs from the type species i. a. by the larger size of its shield, by the shape of the anterior part of the shield, by the small posterior lateral sensory field, and by the ornamentation of the outer face of the exoskeleton.

Geological horizon. — Upper Eodevonian?: Wood Bay series, the upper part of the Lyktan division or the Stjørdalen division.

Localities. — Spitsbergen. E. side of Wood Bay: Mt Sørli, W. slope, 0—500 m (= "between V. Stjørdalen and V. Verdalen"; nos. 434—442, 616); Mt Scott Keltie, N. part, W. slope, ca. 500 m (no. 443). The localities for the specimens hesitatingly placed here are: Mt Sørli, W. slope, 0—500 m (nos. 444—445); Mt Prismefjellet, W. slope, in a fossiliferous horizon about 200 m above sea level (in the Stjørdalen division of the Wood Bay series; nos. 446—447).

All the specimens were collected by the ENS expedition in 1939.

Acrotomaspis sp. 2.

(pl. 104:4.)

The form described here (ENS no. 448) consists mainly of the dorsal exoskeleton of a somewhat incomplete cephalic shield, exposed in ventral view. The length of the shield in the median line is 19.5 mm and the maximum breadth is probably about as great as this length. The shield is very similar to that of *A. trinodis,* the rostral margin of the shield being shaped in the same way, i. e., rather deeply emarginated with protruding antero-lateral corners and a small but distinct median rostral lobe. The lateral angles themselves are not preserved but it seems evident that they were situated far back on the shield, distinctly behind the middle of its length and far behind the level of the orbital openings. The dorsal sensory field is rather small and the lateral sensory fields are very small, as in *A. trinodis;* their third pair is not preserved. The orbital openings are situated very far forward, their distance from the posterior end of the shield is about three times as great as their distance from the apex of the median rostral lobe. The anterior end of the narrow naso-hypophyseal opening lies very near the rostral end of the shield and its distance from the apex of the rostral lobe is probably only half as great as the length of the opening.

Although this specimen is similar to *A. trinodis* it differs from this species in some respects, and very probably represents a species of its own, but owing to its imperfect state of preservation, it cannot be adequately described and is therefore left unnamed. When compared with *A. trinodis* it seems probable that the rostral margin of the shield has not been subject to any great reduction (pushing the rostral margin farther backwards) but that the orbital and the naso-hypophyseal openings have shifted somewhat forwards, and this is supported by the fact that the velar ridge is running from a point laterally to the posterior part of the naso-hypophyseal opening in antero-lateral direction towards the antero-lateral corners of the shield.

This form, along with a *Cephalaspis* sp. (p. 424) is the geologically youngest Cephalaspid found in Spitsbergen.

Geological horizon. — Uppermost Eodevonian or Lower Mesodevonian: Grey Hoek series.

Locality. — Spitsbergen. W. side of Wijde Bay: S. of the Sixth Valley (Sjettedelen), in the coast-profile.

The specimen was collected in 1939 by the ENS expedition.

Genus **Nectaspis** n. gen.

(νηκτος, swimming; ἀσπις, shield.)

Diagnosis. — A cephalaspid genus with cephalic shield is never broader than long. Pre-orbital part of shield rather strongly developed. Real cornua absent, replaced by small lateral angles on shield. Pectoral sinus not developed. Inter-zonal part rather long dorsally, with low median ridge; ventrally not closed. Sensory fields fairly small, consisting of one unpaired dorsal field and three pairs of lateral fields; dorsal field more or less triangular in shape. No pineal plate. Separate openings for nasal and hypophyseal ducts. Two nerve canals entering first lateral sensory field, two running to second, and one to third field. Canal for r. mandibularis trigemini in its course through visceral endoskeleton running between nerve canals to first lateral sensory field, entering oralo-branchial chamber ventrally to first canal. Canal for dorso-lateral superficial vein 3 opening into canal for vena capitis lateralis behind orbit. Strongly developed velar ridge partly separating oral cavity from branchial chamber proper. Truncus arteriosus having passed through ventral notch in postbranchial wall. Superficial layer of exoskeleton continuous, middle layer with radiating canals. Mucous canal system enclosed in exoskeleton, consisting of uniform plexus.

Type species. — *Nectaspis areolata* n. sp.

Remarks. — This remarkable genus is characterized especially by the rather strong development of the pre-orbital part of the shield, the non-development of the cornua, the presence of three pairs of lateral sensory fields, and the strong velar ridge. The more special disposition of the anterior nerve canals for the lateral sensory fields and the canals for the n. trigeminus together with their interrelations, and the disposition of the canal vls_3, show a close conformity with the conditions found in *Boreaspis* as well as in *Kiaeraspis, Axinaspis* and *Acrotomaspis.* If we look for the genera, most closely related to *Nectaspis* we can very probably confine ourselves to either *Boreaspis* (and its allies) or to *Kiaeraspis, Axinaspis* and *Acrotomaspis.* A subdivision of the lateral fields is met with in some species of *Boreaspis,* and occasionally in *Kiaeraspis,* and occurs constantly in *Axinaspis* and *Acrotomaspis.* It is most probable that the presence of three pairs of lateral sensory fields in *Nectaspis* represents a secondary state, and we have only to imagine each of the lateral fields in *Boreaspis* or *Kiaeraspis* being subdivided into three portions to get the picture presented in *Nectaspis.* From the genus *Boreaspis* the present genus differs by the development of the inter-zonal part which is strongly developed in comparison with that of *Boreaspis;* there are no inter-zonal sinus as in *Boreaspis.* As furthermore the oralo-branchial chamber and the exoskeleton are differently developed in the two genera it is seen that the differences between them are rather great, and it seems thus very probable that there is no close affinity between *Nectaspis* and *Boreaspis,* and that *Nectaspis* does not belong to the same line of evolution as *Boreaspis.* The location of the third lateral sensory field on the inter-zonal part of the shield and its shape recall the conditions found in the posterior part of the lateral field in *Kiaeraspis,* in the posterior part of the posterior lateral field in *Axinaspis,* and in the posterior field in *Acrotomaspis.* The shape of the dorsal sensory field is rather similar in *Nectaspis* and these three genera. In the absence of cornua and thus in the narrow shape of the shield as well as in the fairly well developed inter-zonal part *Nectaspis* also shows resemblances to them, but in comparison with these genera and particularly with *Kiaeraspis* and *Axinaspis* the inter-zonal part is comparatively short, and it must be noted that the ventral portion is incomplete medially in *Nectaspis* but is closed in the other genera. *Acrotomaspis* has four pairs of lateral sensory fields, and the distribution of the nerve canals to the posterior field is dissimilar in this genus and in *Nectaspis;* the subdivision of the lateral fields in the two genera must have proceeded along different lines. The strong development of the pre-orbital part of the shield and of the velar ridge as well as the comparatively short inter-zonal part and particularly the feeble development of its ventral portion in *Nectaspis* make it difficult genetically to connect the genus with *Axinaspis* (or *Kiaeraspis* and *Acrotomaspis).* In concluding, we find that *Nectaspis,* although showing many characters, similar to *Kiaeraspis, Axinaspis* and *Acrotomaspis,* and being possibly a distant relative to them, cannot be directly connected with any of these genera.

In the general shape of the cephalic shield the genus is fairly constant but within certain limits there is shown a rather great variation as to some details, e. g. the shape of the sensory fields. The delimitation of the species is very difficult and this is partly due to the (in general) very poor state of preservation of the material. Provisionally three different species are distinguished but the diagnoses of them are fairly vague and the boundaries between them are rather indistinct. With these reservations the genus is considered to contain the very closely related species, *N. peltata, N. areolata,* and *N. dellei.*

As to the geographical and stratigraphical distribution of the genus it will be noted that it is confined to the supposed Upper Eodevonian layers of Spitsbergen. It first appears with a small form *(N. peltata)* in the upper part of the C. Kjeldsen division of the Wood Bay series. In the Lyktan division of the same series the genus is represented by the common and widespread *N. areolata,* and in the Stjørdalen division this species is partly replaced by the rather large *N. dellei.*

1. *Nectaspis peltata* n. sp.

(Fig. 104; pls. 112:2-3; 113:1; 118:3.)

Diagnosis. — A *Nectaspis* species with length of cephalic shield in median line about 18 mm, and maximum breadth of shield 14—15 mm. Rostral part comparatively short with rostral margin broad and slightly convex. Dorsal sensory field narrowly triangular, twice, or somewhat more than twice, as long as broad. Middle lateral field long. Circum-nasal fossa rather deep. Posterior median part of inter-zonal endoskeleton rather narrow.

Holotype. — Cephalic shield (ENS no. 300).

Material. — The material referable to this species consists of seven cephalic shields, ENS nos. 300 (the holotype, pl. 112:2-3), 301—305, 306 (pl. 113:1), all of them in a rather imperfect state of preservation and also somewhat distorted by pressure in the rock. Two specimens (ENS nos. 307—308) are placed here with hesitation.

Description. — Owing to the poor state of preservation many of the feautures of the shields could not be adequately studied. The length of the shield is measured in nos. 300, 303—304 and in them is 18 mm. The distance of the nasal opening from the rostral end of the shield is in the same specimens 8.5, 8.1, and 8.5 mm, respectively; it is 8.6 mm in no. 306. None of the specimens is so well preserved as to allow the breadth of the shield being measured; it is, however, estimated at about 14 mm (no. 303) or 14.5 mm (nos. 300, 306). The height of the shield near the posterior end of the dorsal sensory field is estimated at about 6.5 mm in no. 306. The length of the shield lies well below the average length in *N. areolata,* and does not come up to the length of the smallest shield in that species. The species thus attained a small size.

In general shape the shield is oval with obtusely rounded anterior end. The length of the shield is about one and a third times or one and a quarter times as great as the maximum breadth, and the shield is slightly narrower than in *N. areolata.* The rostral portion of the shield, roofing the buccal cavity, is comparatively short, and the rostral margin is broad; there is no rostral angle. An antero-lateral angle at the transition of the rostral margin into the lateral margins it not at all or only very faintly indicated. The lateral angles seem to be situated more forward than in *N. areolata,* and approximately at the middle of the length of the shield, and at a level with the posterior margins of the orbital openings or slightly behind this level. The inter-zonal part is comparatively long and of the same shape as in *N. areolata;* the dorsal ridge is but very slightly developed. The ventral portion of the interzonal part is incomplete (observed in no. 306). The dorsal sensory field is twice, or somewhat more than twice, as long as broad; it is elongately triangular with the maximum breadth posteriorly; both its lateral and posterior margins are straight; it reaches backwards to the openings for the ductus endolymphatici. The distance of the posterior margin of the field from the posterior end of the shield is slightly greater than the length of the field. In most specimens the shape of the lateral sensory fields could not be determined, but it is seen rather well in no. 306. The anterior field is fairly long, the middle field is long, slightly angularly bent inside the lateral angle of the shield, and the posterior leg of the field thus formed is very short; the posterior field is shorter and slightly broader than the two anterior ones, it is triangular with the lateral margin straight. The intervening spaces between the fields are distinct but not very large. The orbital openings, which are almost circular, are situated about equidistantly from the anterior and the posterior ends of the shield. The openings for the nasal

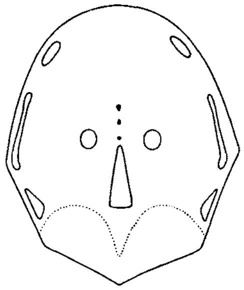

Fig. 104. — *Nectaspis peltata* n. sp. Restoration of the cephalic shield in dorsal view. Mainly after the holotype (ENS no. 300) and ENS no. 306 (the lateral fields). The dotted line indicates the posterior border of the endoskeletal component. × 2.

and the hypophyseal ducts are separated from each other. The circumnasa' fossa is well defined anteriorly, triangular in shape and rather deep on both sides of the opening for the hypophyseal duct.

The minute structure of the exoskeleton is observed in a fragment, hesitatingly placed in this species (pl. 118:3); it agrees with that of *N. areolata* (see this species, p. 545).

The endoskeleton seems to be fairly well ossified but is to imperfectly preserved as to reveal much of its structure. The posterior border of the endoskeletal component in the inter-zonal part is seen in some specimens, its median process seems to be much narrower than in *N. areolata* and ending before the posterior end of the shield.

Remarks. — *N. peltata* differs from the other species of the genus by the small size of its shield and the comparatively short, broad and anteriorly obtusely curved rostral part as well as by the shape of the sensory fields.

The specimens hesitatingly placed here (nos. 307—308) differ from the others by the somewhat greater size of their shields, the most complete shield (no. 307) being 21.5 mm in length. They thus approach *N. areolata* in size but as the shape of the sensory fields and the rostral margin are more in conformity with that of *N. peltata* they are provisionally placed here.

Geological horizon. — Upper Eodevonian: Wood Bay series, the upper part of the C. Kjeldsen division.

Localities. — Spitsbergen. W. side of Wood Bay: Mt Kronprinz, E. slope, opposite Stjørdalen Valley, in a reddish sandstone (nos. 300—306), in a grey sandstone (no. 307, doubtfully placed in this species). E. side of Bock Bay: Mt Kronprinz, W. slope (no. 308, doubtfully placed here).

All specimens were collected in 1939 by the ENS expedition.

2. *Nectaspis areolata* n. sp.

(Fig. 105; pls. 106—111; 112:1.)

Diagnosis. — A *Nectaspis* species with average length of cephalic shield in median line 26 mm, being slightly greater than maximum breadth of shield. Rostral part of shield well developed with rostral margin sharply rounded. Dorso-median portion of inter-zonal part only slightly protracted posteriorly; posterior angle very obtuse. Dorsal sensory field shortly triangular in shape, with broad truncated posterior margin; lateral margins somewhat concave. Lateral fields variable in size, median field rather short, posterior field elongately triangular, slightly curved with pointed anterior end. Orbital openings comparatively large, lying far apart, situated slightly before middle of length of shield in median line. Circum-nasal fossa very broad and shallow. Inter-zonal endoskeleton broad posteriorly.

Holotype. —Cephalic shield (ENS no. 320).

Material. — The material of this species comprises no less than one hundred and six specimens (ENS nos. 309—395, and Pal. Mus. Oslo nos. A24876—A24894); one additional specimen (ENS no. 396) is referred to the same species with some hesitation. All the specimens are represented by cephalic shields only, for the most part in a rather imperfect state of preservation. Only two of them, the holotype (no. 320, pls. 106—109) and no. 321 (pls. 110; 112:1) are perfectly preserved. In many cases the shields are much distorted by pressure in the rock (e. g. no. A24876, pl. 111:3, and no. A24877, pl. 111:4), being thus of a very different appearance even on the same slab owing to the position of the shields according to the direction of pressure. The specimens from Mt Borgen (e. g. no. 360, pl. 111:1; no. 363, pl. 111:2) and from Mt Rebbingen are fairly well preserved with regard to the general shape of the shield. In most of the specimens the endoskeleton is in a very bad state of preservation, the holotype and no. 321 making fine exceptions from this rule.

Description. — The following description is based mainly on the holotype (no. 320) and no. 321 but attention is also paid to the peculiarities of the other shields. The dimensions of the holotype are as follows: The length of the shield in the median line is 24 mm, the breadth between the lateral angles is 19.5 mm, the distance between the rostral end of the shield and the lateral angles is 17.2 mm, and the distance of the nasal opening from the rostral end of the shield 11 mm; the maximum height of the shield (at the posterior end of the inter-zonal part) is 9 mm. The length of the shield in no. 321 is 23.5 mm, and its maximum breadth 17 mm; the height is about 8 mm. The other shields are of somewhat varying size, the length in the median line varies from 21 mm in the smallest specimens to 29 mm in the largest, the average length being 25.9 mm (n = 23);

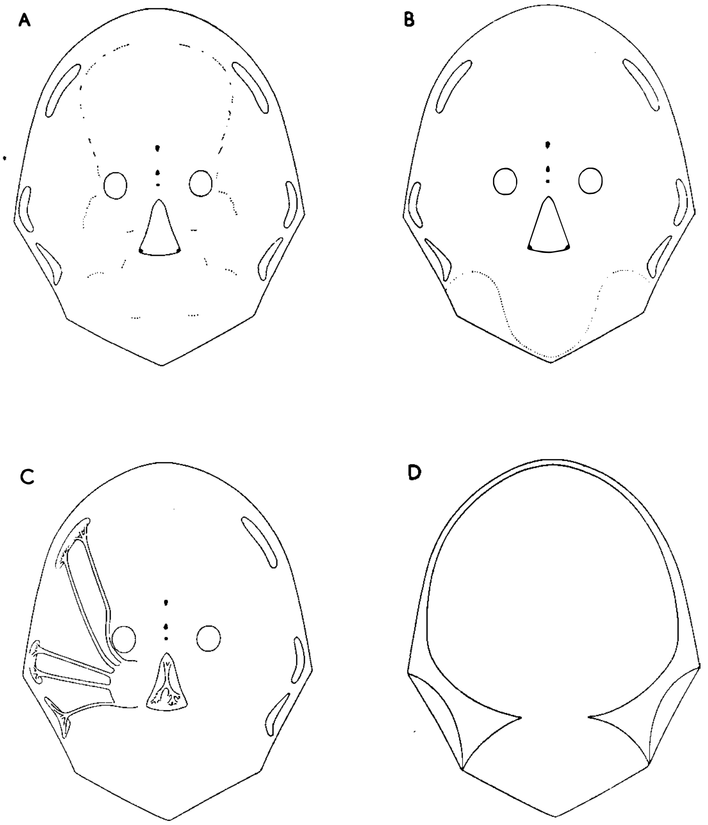

Fig. 105. — *Nectaspis areolata* n. sp. A, B, C, restorations of the cephalic shield in dorsal view, in B, the dotted line indicates the posterior border of the endoskeletal component, in C, the nerve canals to the lateral sensory fields on the left side of the shield as well as the horizontal branches of the nerve canal to the dorsal sensory field are indicated. D, outline of the shield in ventral view. After the holotype (ENS no. 320) and ENS no. 321, D, also after Pal. Mus. Oslo nos. A24876, A24878 and A24893. × 2.

the distance of the nasal opening from the rostral end of the shield varies in fifteen of the same specimens from 9.7 mm to 13.8 mm, and is on an average 12.2 mm. The maximum breadth could be measured in only a few of these specimens; it is about 18.9 mm, varying from 17 to 20.5 mm. As seen from the measurements the shields represent a species of small size.

Taken as a whole the cephalic shield is broadly oval with its length in the median line somewhat exceeding the maximum breadth, being in five specimens on the average one and a third times as great as this breadth. The shield is only slightly decreasing in breadth forwards and the rostral margin of the shield is fairly broad, being sharply curved without any rostral angle. There is a very obtuse, almost imperceptible, antero-lateral angle on each side of the shield at the level of the first lateral sensory field where the rostral margin passes over into the lateral margin, and from this angle towards the lateral angle the margin is almost straight. The obtuse lateral angles of the shield (at the transition of the cephalic shield proper and the zonal part) are situated rather far backwards, and the distance of an angle from the rostral end of the shield is considerably greater than from the posterior end of the inter-zonal part. There are no real pectoral sinus present; in dorsal view the margin between the lateral angle and the postero-lateral angle of the inter-zonal part is almost straight, appearing somewhat concave in ventral view. The inter-zonal part is fairly long and gently decreasing in breadth backwards but somewhat more rapidly than the narrowing of the shield forwards from the lateral angles to the rostral margin; its posterior breadth is somewhat greater than half of the maximum breadth of the shield. The posterior angle of the inter-zonal part projects backwards to some distance behind the postero-lateral angles, the latter are not protracted, and the margin between each of them and the posterior angle is almost straight. In some specimens there are traces of a transverse groove running close to and parallely with the posterior margin of the inter-zonal part. Dorsally this part is provided with a faintly marked broad and flattened median ridge, but in some specimens this ridge is more sharply accentuated at its posterior end. The ventral portion of the inter-zonal part cannot be examined in the holotype, but from what is seen in other specimens (e. g. nos. A24876, A24878, A24893) it is incomplete ventrally, being represented on each side by a narrow, medially pointed bridge situated ventrally to the postbranchial wall, the two bridges being separated by a rather narrow gap. From the postero-median border of the orbital opening there extends a broad, rather faintly marked ridge in posterior direction on to a point just postero-laterally to the dorsal sensory field where it often ends in a very slight tubercle or prominence. This marks the transition from the more horizontal dorso-median portion of the postorbital part of the shield to the downward sloping lateral parts. The dorsal sensory field is well developed, lying in a slight depression in the dorso-median table of the shield; it is triangular in shape; the lateral margins of the field often have an obtuse antero-lateral angle slightly behind the anterior end. The maximum breadth of the field, which lies across its postero-lateral angles, is contained about one and a third times in the length of the field in the median line. The posterior margin of the field is transversely truncated or very slightly convex, the lateral margins are often somewhat concave. The dorsal field reaches backwards to the openings for the ductus endolymphatici (these being situated in the postero-lateral corners of the field), and its distance from the posterior end of the shield is at least one and a half times as great as the length of the field. The anterior lateral field is situated inside of the antero-lateral angle of the shield. The middle field, which is slightly bent with median concavity, lies inside the lateral angle of the shield. The posterior field is very obtusely triangular with the lateral margin somewhat concave and the anterior end somewhat pointed; it lies inside the margin between the lateral and the postero-lateral angles of the shield. The lateral fields are all very narrow; their length as well as the intervals between them is subject to rather considerable variation; the middle field is comparatively much shorter than in *N. peltata.* In the holotype the anterior field is about 4 mm long, the space between the first and second fields is about 4.8 mm; the second field is 3 mm and is separated from the third by a gap of about 1 mm; the third field measures about 3.3 mm. In no. 363 the interval between the first and the second fields is only 2.7 mm and between the second and third about 2.2 mm, and in no. 374 the second and third fields are almost confluent, being separated by a gap of only 0.5 mm. The orbital openings, which are roundedly oval in shape, are comparatively large and placed rather far from the median line of the shield, the interorbital breadth being about three times as great as the transverse diameter of an orbital opening; they are situated very slightly before the middle of the length of the shield in the median line. The circumorbital ridge is rather feebly pronounced. There is no pineal plate; the pineal foramen lies somewhat anteriorly to the fore-end of the dorsal sensory field. The circum-nasal fossa is very broad and rather shallow, it is indistinctly defined anteriorly and posteriorly. The median division of the naso-hypophyseal opening is obliterated in consequence of the lateral margins of the exoskeleton, bordering this division, meeting; the line of fusion is often marked by a suture; in the holotype, however, even this suture has disappeared. The nasal opening is situated on a small elevation and the opening for the hypophyseal duct, which lies rather far in front of the nasal opening, is also located on a rather faintly marked prominence.

The exoskeleton is well developed. The superficial layer is continuous and, as far as can be seen, smooth; it is perforated by the comparatively large, very closely set pores of the mucous canal system. This system is enclosed in the exoskeleton and developed as a fine-meshed network. Radiating vascular canals have been observed in the middle and posterior parts of the shield and are disposed in distinct separate fascicles. The vascular areas formed by them are very large in proportion to the size of the shield. Very long radiating canals emanate from a point on the slight prominence postero-laterally to the dorsal sensory field.

Some of the grooves of the sensory line system are observed in the holotype and in no. 321. The infraorbital line does not enter the lateral sensory fields but curves in median direction slightly medially to the antero-median corner of the first field.

The endoskeleton is strongly ossified with well developed perichondrial bone-layers in the holotype and in no. 321. The extent backwards of the endoskeletal component in the shield is shown in fig. 105B; its median posterior process is very broad and reaches backwards almost to the posterior end of the inter-zonal part. With regard to the disposition of the cranial nerve canals, it can be noted that the r. mandibularis trigemini in some specimens was lodged in a canal of its own all the way from the antero-median part of the labyrinth cavity and did not traverse the orbit; its canal *(V_3)* in the visceral endoskeleton runs behind the canal sel_1, and somewhat postero-medially to the anterior lateral field passes down to the oralo-branchial chamber ventrally to that canal. The canal *VII* lies in its course through the visceral endoskeleton just in front of the canal sel_2. The anterior lateral field is supplied with two nerve canals *(sel_1, sel_2);* the middle field likewise with two canals *(sel_3, sel_4),* and the posterior field receives one nerve canal *(sel_5),* which within the field divides into three branches. The two nerve canals of the dorsal sensory field join to an unpaired canal which almost immediately divides into one anterior and two posterior horizontal canals. The canal *vcl* is seen in no. A24886; it starts from the postero-dorso-lateral part of the orbit and runs in a straight posterior direction; at some distance behind the orbit it receives the canal vls_3. The superficial vascular canals are very wide especially in the posterior part of the shield and anastomose with each other, making it rather difficult to determine the courses of the different main canals. The postbranchial wall is almost vertical in its dorsal part but sloping posteriorly in the ventral parts; the truncus arteriosus crossed the wall by a large ventral notch.

Remarks. — Most of the specimens referred to this species are very poorly preserved and have been grouped together mainly on account of the size, proportions and general appearance of the shields. When, however, details in the different shields could be examined, they seem to be rather similar. All the specimens in question have thus been considered as belonging to but one species.

N. areolata seems to be distinguished from its congeners by the rather constant size and the general shape of its shield, as well as by the rather sharply curved rostral margin and the shape of the dorsal sensory field.

Geological horizons. — Upper Eodevonian ?: Wood Bay series, the Lyktan division, the lower part of the Stjørdalen division.

Localities. — Spitsbergen. E. side of Dickson Bay: Mt Lyktan, S.E.slope (towards Nathorst Valley; nos. 309—323), W.slope (no. 324), Fiskedalen Valley (nos. 325—331); Mt Rebbingen ("the Mt. N. of Fiskedalen"), S.W. slope (nos. 332—351); Mt Triplex, N. side, Culm Valley (nos. 352—358). W. side of Dickson Bay: Mt

Borgen, N. part (nos. 359—371). N. of Dickson Bay: Perched Block Mtn (nos. 392—393). E. side of Ekman Bay: the Valley N. of Mt Garborg (nos. 372—386); the Mountain N. of Mt Garborg, W. slope (no. 287); the second Mountain N. of Mt Garborg, S. part, the red ridge (nos. 388—389), N.W. slope (nos. 390—391). W. side of Wijde Bay (West Fiord): Mt Errol White (= "the Mtn S. of Sneugle Valley"; nos. A24876—A24894), E. slope, fossiliferous horizon about 125 m (no. 396, hesitatingly placed in this species). E. side of Wood Bay: Stjørdalen Valley, S. side (nos. 394—396).

The specimens nos. A24876—A24894 were collected by Th. Vogt's expedition in 1928, the others by the ENS expedition in 1939.

3. *Nectaspis dellei* n. sp.

(Fig. 106; pl. 113:2-4.)

Diagnosis. — A comparatively large *Nectaspis* species with average length of cephalic shield in median line 39 mm and with maximum breadth of shield distinctly less than this length. Rostral margin fairly broad, sharply curved. Posterior angle obtuse but distinct. Dorsal sensory field small, triangular or trapezoidal (posterior margin angulate). Posterior lateral field not curved. Orbital openings comparatively small, lying distinctly behind middle of length of shield in median line. Circum-nasal fossa well developed, rather deep posteriorly.

Holotype. — Cephalic shield (ENS no. 400).

Material. — In this species I place thirty-seven specimens, ENS nos. 397—399, 400 (the holotype, pl. 113:3); 401—402, 403 (pl. 113:4), 404—405, 406 (pl. 113:2), 407—433. The specimens consist of imperfectly preserved cephalic shields or fragments of such shields, all of them being more or less distorted by pressure in the rock.

Description. — Owing to the imperfect state of preservation none of the specimens shows the real shape of its shield, and many of the structural details are obscured; the following description must thus be considered as only tentative and provisional.

The average length of the cephalic shield in the median line seems to be 39 mm, varying from 34 mm to about 44 mm after measurements on a few not very much distorted specimens. Compared with the other described species of the genus this species is rather large.

Taken as a whole the shield is broadly oval with rounded anterior, and more pointed posterior end. To judge from conditions in specimens relatively unaffected by pressure the length of the shield seems to be distinctly greater than the maximum breadth of the shield. The rostral margin is fairly broad and convex. The lateral angles are situated somewhat posterior to the level of the orbital openings and

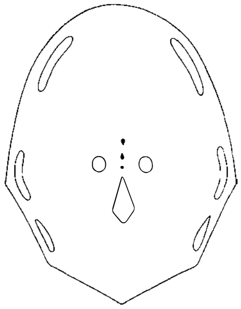

Fig. 106. — *Nectaspis dellei* n. sp. Attempted restoration of the cephalic shield, dorsal view; mainly after the holotype (ENS no. 400) and ENS no. 416. Nat. size.

thus distinctly behind the middle of the length of the shield. The posterior angle of the inter-zonal part is rather distinct but obtuse, yet often a little less so than in *N. areolata.* The inter-zonal part is incomplete ventrally as is shown in no. 406. The dorsal sensory field is comparatively very small and situated rather deep in an elongated depression bordered by rather strong ridges running in posterior direction from the postero-median corners of the orbital openings. The field is triangular or trapezoidal in shape, its breadth across the postero-lateral corners is about half as great as its length in the median line. The posterior end of the field is often more or less protracted backwards and the posterior margin it thus angulate. The distance of the posterior end of the field from the posterior end of the inter-zonal part is at least one and a half times as great as the length of the field. The lateral fields are small and narrow; their length is rather variable; in no. 416 the anterior field is 5.5, the middle 4, and the posterior field 3 mm long, the interval between the anterior and the middle fields is about 4 mm, and between the middle and the posterior fields only about 1 mm. In nos. 400 and 401 the middle field measures 6 mm and the gap between that and the posterior field is 2 mm; in no. 404 the middle field is 8 mm long. In general the distance between the middle and the posterior field is rather inconsiderable. The middle field is often distinctly angulate with about equal legs and medially directed concavity; the posterior field is elongate with pointed anterior, and rounded posterior end. The orbital openings which are strikingly small in proportion to the size of the shield are situated behind the middle of the length of the shield in the median line; they are circular or slightly oval. A suture-line from the nasal opening to that of the hypophyseal duct indicates the united borders of the middle division of the original naso-hypophyseal opening. The circum-nasal fossa is well-developed and rather broad, and has rather indistinct borders anteriorly but is well defined and rather deep on both sides of the nasal opening.

Nothing can be said of the minute structure of the exoskeleton.

The endoskeleton seems to have been rather well ossified but in most specimens it is destroyed or imperfectly preserved; only occasionally some of the internal structures are seen. The disposition of the canals of the principal superficial nerves and vessels seems to be as in *N. areolata.*

Remarks. — *N. dellei,* which reminds rather much of *N. areolata,* is distinguished principally by the size of its cephalic shield, the small orbital openings, and the shape of the dorsal sensory field.

The species is named in honour of Dr. N. Delle, formerly at Riga, well-known authority on Devonian stratigraphy, member of the ENS expedition in 1939.

Geological horizon. — Upper Eodevonian ?: Wood Bay series, the Stjørdalen division.

Localities. — Spitsbergen. E. side of Wood Bay, Mt Sørli, W. slope (= "between V. Stjørdalen and V. Verdalen"), 0—500 m (no. 397); Stjørdalen Valley, S. side (nos. 398—433).

All specimen were collected by the ENS expedition in 1939.

Remarks on other Osteostraci.

As indicated in the remarks to the family Cephalaspididae (p. 242) the genera allied to *Hemicyclaspis* are regarded as forming a subfamily of their own, Ateleaspidinae (cf. Heintz 1939; Robertson 1945; Denison 1951a). This subfamily forms a natural group of evidently closely related forms, but it is not easy to give a sharp definition. In most characteristics it approaches the sub-family Cephalaspidinae with which it agrees i. a. in the disposition of the first nerve canal for the lateral sensory field and the course of the infraorbital sensory line. The main differences lie in the absence of cornua and the development of the pectoral fin in which the subfamily is said to exhibit primitive traits. The genus *Ateleaspis* is considered to represent a primitive stage in the evolution of the pectoral fin (Heintz 1939), and the conditions in these respects in the other genera are thought to have been derived from this stage, showing a differentiation of the fin originating from the lateral fin fold. It is, however, surprising to find these different evolutional stages among geologically so young forms, inasmuch as already in the Lower Ludlow Osteostraci forms are present which possess well developed cornua and, without doubt, well developed and differentiated pectoral fins. The different stages in the development of the pectoral fin in the Ateleaspidinae must, however, not necessarily be taken as representing a progressive differentiation of the fin; they can be interpreted as representing a regressive development, and the conditions in *Ateleaspis* are then not primitive but derivative. The recorded fossils are as yet too few or too imperfectly known as to allow us to see clearly or even to surmise the different phyletic lines in the Osteostraci and to interpret correctly the morphological stages, shown in the fossils, or to understand their real significance.

The subfamily Ateleaspidinae includes at present the following genera: *Hemicyclaspis* Lankester (1870a; incl. *Hemiteleaspis* Westoll, 1945[1]); *Ateleaspis* Traquair (1899b); *Aceraspis* Kiær (1911); *Hirella* Cossmann (1920; = *Micraspis* Kiær 1911, n. Dejean 1835, Hope 1840). *Witaaspis,* placed here by Denison (1951a), is considered not to belong to this subfamily.

As mentioned before (p. 240) some of the genera *(Thyestes, Didym-*

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[1] According to verbal information from Dr. E. I. White *H. heintzi* Westoll is a *Hemicyclaspis* sp. indet.

aspis, Sclerodus) included in the family "Cephalaspidae" by Stensiö, show several features in the cephalic shields, which are unknown in the rest of the genera, and I therefore considered it best to exclude them from this family. The aberrant features referred to are connected especially with the disposition of the first nerve canal *(sel_1)* for the lateral sensory field. In the genera mentioned this canal runs in almost straight direction from the labyrinth cavity towards the lateral field and is placed rather far backwards, considerably behind the orbit. It lies distinctly behind the canal for the r. mandibularis V; it is furthermore said (Stensiö 1932, pp. 39, 45, 152, 164, 169, 171, 173—174, 175, 179) to be situated behind the canal for the n. facialis but the evidence brought forward in this matter seems not conclusive (cf. Stensiö 1932: the canal V_2 in pls. 50:3; 51:2 and the canal V_2 in pl. 50:4 are most probably not canals for the r. mandibularis, and the canal *VII* in pl. 51:2 is possibly the canal for this nerve; the groove V_2 in pl. 52:2 takes a place corresponding to that of the groove *VII* in pl. 53:5). The disposition of the canal sel_1 is to some degree correlated with the extent of the lateral sensory field which generally reaches much less forward than in Cephalaspididae. In this connection we can mention the fact, already pointed out by Stensiö (1932, pp. 75, 152) that the lateral fields never extend backwards on to the cornua; in *Sclerodus* they are short and straight, in *Thyestes* they end posteriorly considerably in front of the pectoral sinus and are provided with a more or less distinct postero-median corner, in *Didymaspis* they end on the antero-lateral portion of the inter-zonal part of the shield and are provided with a lateral corner. Another differential character, of less importance, lies in the course of the canal for the postorbital division of the v. capitis lateralis, which in Cephalaspididae runs in almost straight posterior direction from the posterior corner of the orbit but in the present genera issues from the postero-lateral corner of the orbit and then runs first for a short distance in postero-lateral direction before it turns backwards, its posterior course being more or less straight *(Sclerodus,* Stensiö 1932, pl. 52:2) or sigmoidally bent *(Thyestes, Didymaspis,* Stensiö 1932, fig. 13; pls. 50:2-3; 51:2; 55:1). The course of the canal is thus somewhat similar to that in *Tremataspis* (Stensiö 1927, pl. 60; Robertson 1938a, pl. 1:6; this paper, fig. 108). An additional difference is exhibited by the course of the infraorbital sensory line; in Cephalaspididae the line runs from the side of the orbital opening in antero-lateral direction towards the anterior part of the lateral sensory field, which it (except in *Nectaspis,* as far as known) traverses in turning first in anterior, later in median direction; it then leaves the field and generally meets its fellow of the opposite side of the shield between the anterior ends of the lateral sensory fields. In *Thyestes,* however, the infraorbital line runs in anterior or antero-median direction from the lateral side of the orbital opening and turns medially already somewhat in front of the circum-nasal fossa; it lies thus in its entire length far medially to the lateral sensory field, running almost above the lateral and anterior margins of the endocranium (Robertson 1940b, pl. 1:1; this paper, fig. 107). The course of the line is somewhat similar to that in *Tremataspis,* a fact which has already been emphasized by Robertson (1940b, p. 469; 1945, pp. 172, 182). In *Thyestes* we find also an anterior marginal line (Robertson 1940b, p. 469; pl. 1:1) and an extra-lateral line (fig. 107); the former line is also observed in *Saaremaaspis* (Robertson 1938b, p. 492, fig. 2; Denison 1951a, fig. 29C) and in *Tremataspis* (Robertson 1938a, p. 197, fig. 1) and the second one in this latter genus and in *Cephalaspis signata, C. aarhusi* and *C. broughi* (p. 188). The genus *Didymaspis* seems to be rather aberrant with regard to the course of the infraorbital line (Stensiö 1932, p. 174, fig. 61A; pl. 55:3) but I have seen a specimen of *Thyestes verrucosus* (Pal. Mus. Oslo no. A003) in which there exists a very small antero-lateral branch of the infraorbital groove, and thus the conditions in this specimen seem to be rather intermediate between the normal type and that in *Didymaspis.* The antero-lateral branch constitutes most probably a part of the anterior marginal sensory line. In *Sclerodus* the sensory line system is unknown.

Didymaspis differs from the two other genera by the very strong development of the trunk division of the cephalic shield, which resembles that of *Tremataspis, Dartmuthia,* and others. The nature of the pectoral sinus seems not to be wholly clear in so far as it has not been plainly shown that they really housed pectoral fins (cf. Westoll 1945, p. 350; Denison 1951a, p. 185). As its relationship to other Osteostraci is obscure, the genus is for the time being best placed in a family of its own (cf. Robertson 1945): Didymaspididae (with the only genus *Didymaspis* Lankester, 1867).

Sclerodus differs widely from all other Osteostraci by the extreme development of the cornua and by the fenestrated margin of the shield; unfortunately it is imperfectly known, and it is uncertain whether it possessed pectoral fins or not. It is apparentliy not very closely related to any of the known genera of the order, and is most conveniently placed in a separate family (cf. Berg 1940; Denison 1951a): Sclerodontidae (single genus: *Sclerodus* Agassiz, 1839).

The genus *Witaaspis* was based (Robertson 1939a) on *Cephalaspis schrenkii* Pand. (a second species, *W. patteni* Robertson 1940a, is by Denison 1951a, p. 158, synonymized with the type species). As far as known (Pander 1856; Schmidt 1894; Rohon 1892, 1895, 1896a; Stensiö 1927, pl. 48:2; Robertson 1939a, 1945; cf. also Denison 1951a, pp. 186—187, figs. 23B, 30B) *W. schrenkii* agrees rather well with

Fig. 107. — *Thyestes verrucosus* Eichw. Imperfect cephalic shield; parts of the dorsal exoskeleton and of the endoskeleton in ventral view. Stained with alizarin. Pal. Inst. Uppsala no. O80 (same specimen as in Stensiö 1927, pl. 48:1). × 4.

elc, extra-lateral sensory line; *ifc,* infraorbital sensory line; ifc_1, anterior division of the infraorbital sensory line; *lc,* main lateral line on trunk division of the cephalic shield; lc_1, cephalic division of the main lateral line; *scc,* scapular sensory line; sel_1, canal for the first nerve of the lateral sensory field; *stc,* supratemporal sensory line; V_2, canal for the r. maxillaris V; V_3, canal for the r. mandibularis V.

Thyestes in many characters. The canal sel_1 is straight and runs behind the orbit; the canal V_3 lies distinctly in front of the canal sel_1; the disposition of the canal *VII* is uncertain but it seems unlikely that it could have passed in front of the canal sel_1; the canal for the post-orbital division of the v. capitis lateralis issues from the postero-lateral corner of the orbit and is, in its posterior course, sigmoidally bent. (From the limited material at my disposal it is, however, evident that the nerve canals V_2, V_3 and sel_1 are not disposed in such a way that the restoration by Denison, 1951a, fig. 23B, could have been based on them). The course of the infraorbital sensory line is on the whole as in *Thyestes.* The lateral sensory fields are better developed than in *Thyestes;* they reach rather far antero-medially, and end posteriorly on the zonal part of the shield immediately in front of the pectoral sinus with a postero-medially directed process. The inter-zonal part of the shield is much shorter than in *Thyestes.* Cornua are present but very short; in their general shape, however, they remind somewhat of those in

Thyestes verrucosus (I can not find that the shape of the cornua or the pectoral sinus agree with the restorations by Denison, 1951a, figs. 23B, 30B). I think that *Witaaspis* is to be regarded as allied to *Thyestes.*

"Procephalaspis" oeselensis (Robertson 1939b; cf. Denison 1951a, p. 189, figs. 20, 23A, 28A, 30C; 1951b, pp. 210—211, figs. 35C, 37A) is very imperfectly known. The course of the infraorbital sensory line agrees with that in *Thyestes* and *Witaaspis.* The lateral sensory field is short, ending considerably in front of the pectoral sinus (Robertson 1939b, fig. 1; the restorations by Denison are inconsistent with this figure as regards the shape of the lateral field and its relation to the cornua and the pectoral sinus). If the restoration of the nerves by Denison is correct the species is in this respect *Cephalaspis*-like. The species is provisionally and with some doubt placed systematically near to *Thyestes* and *Witaaspis.*

The genus *Thyestes* is considered the type genus of a separate family, Thyestidae (cf. Rohon 1896b), in which the genera *Thyestes* Eichwald (1854) and *Witaaspis* Robertson (1939a) and, hesitatingly, the species *"Procephalaspis" oeselensis* are placed. It is possibly closely related to the family Cephalaspididae.

Dartmuthia (with the species *D. gemmifera* Patten, 1931; cf. Robertson 1935a; Wängsjö 1944; Denison 1951a, 1951b) is still very imperfectly known with regard to its endoskeletal characters. From the branching of the nerve canals in the lateral sensory field it was inferred that the canals are five in number, the anterior one being disposed in the same way as in *Thyestes* in relation to the orbit (Wängsjö 1944, p. 360; the nerves are also so restorted by Denison 1951a, fig 22C). The infraorbital sensory line (Robertson 1935a, p. 332; fig. 2; Denison 1951a, fig. 29D; and own observations) runs just as in *Thyestes, Tremataspis* and others (see also Robertson 1940b, p. 469; Denison 1951a, figs. 29—30) and thus differently from that in the real Cephalaspids. The structure of the exoskeleton is most remarkable as it is said (Denison 1951b) to be quite differently developed on the dorsal and on the ventral side of the shield; it is *Tremataspis*-like in the development of the basal layer and is said to be so in the whole ventral exoskeleton; otherwise it shows features distinguishing the non-tremataspid Osteostraci. In the general shape of its cephalic shield *Dartmuthia* resembles *Tremataspis;* the shield is very long; it lacks every vestige of cornua, cornual angles or pectoral sinus, and as there is no place for a fossa articularis it was devoid of pectoral fins. The plates of the oralobranchial fenestra are rather large as in *Tremataspis* (Robertson 1935a, pp. 329—330; fig. 1), thus differing from those in *Thyestes,* which are small (Stensiö 1932, p. 170). The lateral sensory field is rather long.

Saaremaaspis (Robertson 1938b, p. 488) was founded as a new genus on *Tremataspis mickwitzi* (Rohon 1892, p. 56). *Rotsiküllaspis obrutchevi* (Robertson 1938b, p. 489) is by Denison (1951a, p. 158) considered conspecific with *S. mickwitzi* (I wholly agree with Denison that Robertson's restoration of *S. mickwitzi* is based on an imperfect specimen but as far as I can see the posterior margin of the holotype shield is mostly intact and the length of the shield is about 28 mm; it had no cornua; the two specimens of the original material of *S. mickwitzi* are somewhat broader than the holotype of *R. obrutchevi,* but the difference is possibly of no systematic importance). The differences between *Saaremaaspis* and *Dartmuthia* seem to be rather insignificant and mainly referring to a different development of the minute structure of the exoskeleton. *Saaremaaspis* can perhaps not be maintained as an independent genus.

Dartmuthia and *Saaremaaspis* are placed together in a family of their own, Dartmuthiidae (cf. Patten 1931; Robertson 1939b; 1945; Denison 1951a).

The genus *Oeselaspis* was based (Robertson 1935b) on the species *Didymaspis pustulata* (Patten 1931); it is still imperfectly known, especially with regard to its internal characters, although Denison (1951a, fig. 22B) has given a restoration of cranial nerves and vessels. The cephalic shield forms a strongly developed carapace as in *Tremataspis* and Dartmuthiidae; it lacks pectoral fins (and pectoral sinus). The infraorbital sensory line runs as in *Thyestes, Tremataspis* and others (Denison 1951a, fig. 29B). In the restoration of the cranial nerves and vessels by Denison the four nerves for the lateral sensory fields (of which there are two on either side of the shield, as in *Tremataspis)* are differently distributed on the left and right side, indicating that the conditions are variable in different specimens of the species, a most exceptional case; the posterior dorso-lateral superficial vein is *Tremataspis*-like. Awaiting more detailed descriptions of the actual conditions of the internal structures in the fossils, which will possibly give a clear exposition of the organisation of the animal and settle its relationship to other genera of the order, *Oeselaspis* is here provisionally placed in the Tremataspididae (following Denison 1951a; cf. Berg 1940).

Tremataspis is a well known genus and has been the object of many inquiries into its structure and its systematic affinities (see Gross 1935; Robertson 1938a, with bibliography; Wängsjö 1944; Westoll 1945; Denison 1947; 1951a; 1951b; Bölau 1951). Although the external morphology of the cephalic shield as well as the minute structure of the exoskeleton is well known, and also rather much of the endoskeleton (Stensiö 1927; Robertson 1938a; Denison 1951a) much remains to be done with regard to the internal anatomy of

Tremataspis. As I have at my disposal some specimens with a partly well preserved endoskeleton, I can here give a few supplementary notes on the internal anatomy of the genus (cf. fig. 108). The specimens belong to the species *T. mammillata* Patten.

The canal for the postorbital division of the v. capitis lateralis *(vcl)* issues from the postero-dorso-lateral corner of the orbit and runs backwards in a lateral bend peripherally to the non-ossified division of the endocranium for the labyrinth cavity. Somewhat behind the orbit it receives a canal *(vls),* probably corresponding to the canal for the third dorso-lateral superficial vein (*vls*$_3$) in the Cephalaspids, and some distance behind this point another large vein canal *(vlsp)* opens into the canal. This canal *vlsp* is composed of branches from the region between and medially to the two lateral sensory fields (the branches are largely removed in the specimen figured but they can be seen in Robertson 1938a, pl. 1:6); the canal *vlsp* is evidently equivalent to the to the dorso-lateral superficial vein canals behind *vls*$_3$ in the Cephalaspids. The canal *adl* runs from the region immediately antero-laterally to the orbit in lateral and, further distally, in a postero-lateral direction, somewhat laterally to or very close to the lateral margin of the anterior lateral sensory field. The canal very probably is a strongly developed branch of the canal for the a. adorbitalis. In some specimens it is very difficult to follow the course of the vascular canals owing to the fact that the vein canals in some places (e. g. postero-laterally to the orbital openings) are much widened so that large vein sinus are formed. The anterior lateral sensory field is supplied with two nerve canals (*sel*$_1$, *sel*$_2$); they are separated from each other at least as far medially as to the canal *vcl,* and they very probably represent two independent nerve canals. In relation to the orbit the anterior one is disposed in the same way as in *Thyestes* and others, but its relation to the canals for the r. mandibularis and the n. facialis is unknown. Also the posterior lateral sensory field, as revealed by this specimen, is supplied with two nerve canals (*sel*$_3$, *sel*$_4$) and not one as I have stated previously (Wängsjö 1944, p. 360; cf. Denison 1951a, pp. 166, 181); in median direction the canals could be followed to a point where they disappear under the canal *vcl;* proximally they run very closely to each other, further distally the anterior canal diverges in its course from the posterior one, and not until just before it enters the lateral field the canal turns in postero-lateral direction and again approaches the posterior nerve canal. The disposition of these posterior nerve canals can possibly be explained rather by assuming that the sensory fields are in a state of reduction than that they are expanding (in the latter case we should have expected to find one nerve canal which showed strong distal ramification).

Considering what is known of the morphology of *Tremataspis*

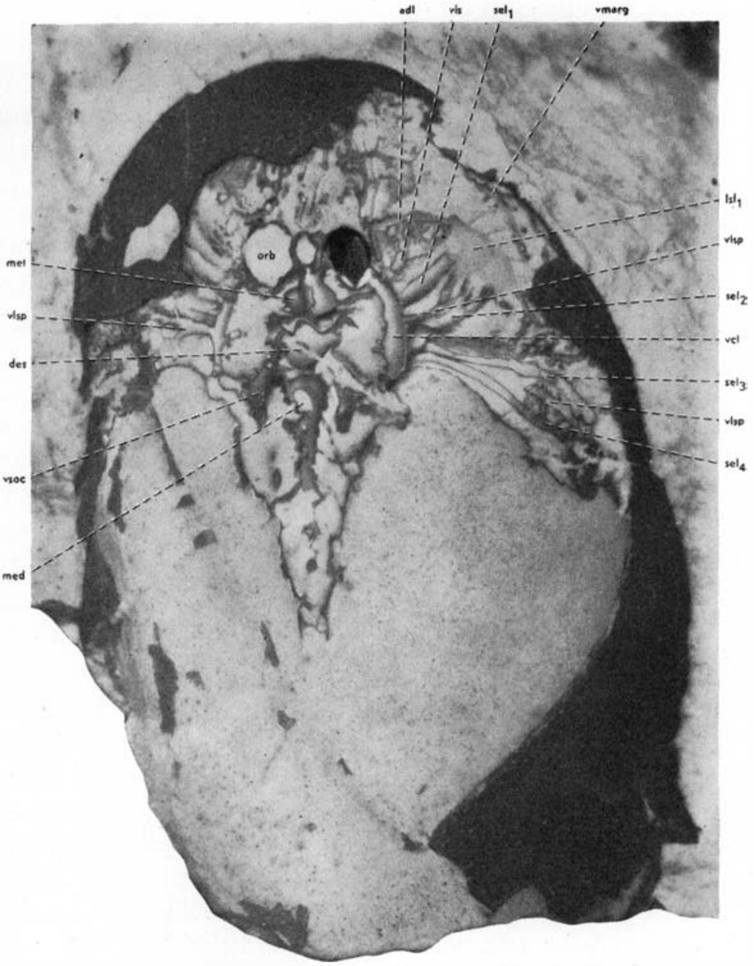

Fig. 108. — *Tremataspis mammillata* Patten. Cephalic shield in dorsal view; left side distorted. Endoskeleton rather well ossified. Exoskeleton partly removed and shield somewhat dissected so that several internal structures are exposed. Pal. Inst. Uppsala no. O98. About × 4.

adl, canal for a lateral branch of the a. adorbitalis; *des,* common canal for the nerves for the dorsal sensory field; lsf_1, anterior lateral sensory field; *med,* division of the cranial cavity for the medulla oblongata; *met,* division of the cranial cavity for the cerebellum; *orb,* orbit; sel_1—sel_2, canals for the nerves of the anterior lateral sensory field; sel_3—sel_4, canals for the nerves of the posterior lateral sensory field; *vcl,* canal for the v. capitis lateralis; *vls,* canal, possibly corresponding to the canal for the dorsolateral superficial vein 3 in the Cephalaspids; *vlsp,* canal for a large posterior dorsolateral superficial vein; *vmarg,* canal for the v. marginalis; *vsoc,* occipital vein sinus.

(especially such characters as the long carapace, the structure of the exoskeleton, the presence of two pairs of lateral sensory fields and their nerve supplies) it seems more probable that the genus represents a specialized offshoot from the main stem of the Osteostraci (cf.

Obruchev 1945) than that it exhibits primitive features (cf. Westoll 1945; Denison 1951a).

However, Westoll (1945) and Denison (1951a) have argued strongly for the proposition that the forms with a long and strongly developed carapace and devoid of pectoral fins represent a primitive stage from which the other forms with pectoral fins and cornua have evolved. In the oldest known Osteostraci faunas, from Saaremaa (Lower Ludlow), there are known a number of forms with long carapace and without pectoral fins but we find there also forms with short cephalic shields, well developed pectoral sinus and cornua (and thus certainly with well differentiated pectoral fins). The strong carapace in these early forms is a continuous structure without any apparent indications of having been composed of fused trunk scales. This is, however, the case in *Kiaeraspis* which among geologically young forms has the longest cephalic shield. We do not know how much of the trunk was encased in the shield of *Kiaeraspis* but in *Tremataspis* it is probable that it must have been the main part of the trunk and that only the caudal region, or somewhat more, of the trunk, was unprotected by the carapace. As has been pointed out by Damas (1943, pp. 264—265) with regard to the anterior myotomic musculature in the Cephalaspids and the Petromyzonts it seems highly probable that under the cephalic shield this musculature was degenerated or had disappeared. If we assume that the carapace, inherited from the ancestors, was reduced in later forms such as *Cephalaspis,* it seems most improbable that the trunk scales which arose from the desintegration of the carapace would have assumed a disposition which was similar to that of the posterior part of the trunk, reflecting, as it evidently does, the shape of the myomeres (cf. Lankester 1870a, p. 41; Stensiö 1932, p. 59; cf. also Kiær 1911, p. 18; 1924, pp. 94—97). It is most probable that the heavy-armoured forms were specialized offshoots which did not give rise to forms with short cephalic shields. The lateral fin-fold which must have been a very ancient feature in the vertebrates, present in the ancestors to both the Agnatha and the Gnathostomata, was in such forms as *Tremataspis* in a more or less reduced state, and it certainly is not found in this genus as an incipient structure (cf. Denison 1951a, pp. 174—178). Whether the ancestors of *Tremataspis* had the anterior part of the fin fold differentiated into a pectoral fin or not, cannot be decided. It can furthermore be noted that the forms without pectoral fins certainly must have had the tail developed differently from those forms provided with such fins (cf. p. 235).

Tremataspis is maintained in a family of its own, Tremataspididae.

In default of something better, the following preliminary arrangement of the different families in the order Osteostraci is given to convey an approximate idea of the position among the Osteostraci of the Cephalaspids treated in this paper (subfamily Cephalaspidinae):

Family	Tremataspididae	*(Tremataspis, ? Oeselaspis)*
”	Dartmuthiidae	*(Dartmuthia, Saaremaaspis)*
”	Didymaspididae	*(Didymaspis)*
”	Sclerodontidae	*(Sclerodus)*
”	Thyestidae	*(Thyestes, Witaaspis, ? “Procephalaspis”)*
”	Cephalaspididae	
	Subfamily Ateleaspidinae	*(Ateleaspis, Aceraspis, Hirella, Hemicyclaspis)*
	” Cephalaspidinae	*(Cephalaspis* and others)

Some comments upon other agnathous vertebrate groups in relation to the Osteostraci.

The other groups which are now generally included in the division Agnatha, and thus supposed to be closely or distantly related to the Osteostraci, are the Anaspida, the Heterostraci, including the Thelodonti, and the recent Cyclostomata as well as the newly erected order Euphanerida.

Anaspida. After the fundamental work by Kiær (1924) on the Norwegian Anaspids and the structure and organization of the group, and the subsequent comparative morphological studies by Stensiö (1927, pp. 309—314; 1932, pp. 180—183; 1939) on these forms it seems now beyond any reasonable doubt that the Anaspids and the Osteostraci constitute two closely allied groups among the Ostracoderms (cf. also Stetson 1927; White 1935a; Heintz 1938; Gross 1939; Moy-Thomas 1939; Berg 1940; Obruchev 1945; Romer 1945; 1946; etc.).

The most obvious and significant resemblance between them lies in the presence of a median unpaired naso-hypophyseal opening with the same topographical relations to the orbits and to the pineal opening, indicating that in both groups the rostral part of the head was formed in a similar way, and not by the ethmoidal region but, as in modern Cyclostomes, by an excessive development of the prenasal visceral parts (the “upper lip”, the “post-hypophyseal fold”).

Other similarities are found in the scale-covering of the trunk: similar overlapping and articulation of the scales, high lateral scales, dorsal unpaired, hollow scales (spines or scutes), agreements in the structure of the pectoral plate (and spines behind it) in the Anaspida and the ventro-lateral scales in the Osteostraci, both belonging to the lateral fin-fold.

As differential features between the two groups can be counted: the composition (in part?) from independent scales of the exoskeleton in the head of the Anaspida, which in the Osteostraci forms, dorsally and laterally, part of a continuous cephalic shield; the branchial openings, which have in the Anaspida shifted rather far backwards compared with those of the Osteostraci; the general form of the body, the shape of the caudal fin and the transformed anterior part of the lateral fin-fold; the absence in the Anaspida of sensory fields; etc.

Nothing is known of the endoskeleton in the Anaspida and thus very little of their inner structures. The external branchial openings (six to fifteen on each side) form a series of very closely lying, rounded, apertures far back on the sides of the head. Though nothing is known of the structure of the gills, it is assumed that they were sac-like as in modern Cyclostomes. It seems very probable that the efferent ducts from the gill-sacs were rather long (Kiær 1924, p. 90), and that their external openings were crowded together much in the same way as in *Paramyxine* (Dean 1904, figs. 2, 4; pl. 1:3-4); if this be so we cannot, from the position of the gill-openings, infer anything as to the position and branchiomeric significance of the gill-sacs (cf. Stensiö 1927, pp. 311—312).

The development in the Anaspida of a hypocercal caudal fin was evidently correlated with the non-development of real, movable, pectoral fins and with the shape of the fusiform body, and is regarded as an adaptive character without any great phylogenetic value (cf., however, White 1935a, p. 431).

The mode of living of the Anaspida differed widely from that of the Osteostraci in so far as the Anaspida certainly were nectonic forms and possibly plankton-feeders (Kiær 1924, p. 91; Stensiö 1927, p. 313; Moy-Thomas 1939, p. 24; Harris 1936, pp. 491—492; Robertson 1951b, p. 493).

Heterostraci. — In the Heterostraci (Pteraspidomorphi; Pteraspides) are generally placed two wholly different groups, i. e. the Heterostraci proper (Pteraspida)[1] and the Thelodonti (Coelolepida). Although they are regarded by most authors as allied groups, they have very few characteristics in common, and we know in fact very little about the structure of the latter group. Their position as agnathous

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[1] Including the Poraspididae, Cyathaspididae, Traquairaspididae, Amphiaspididae, Pteraspididae, and Drepanaspididae. Usually *Astraspis* and *Eriptychius* (from the Upper Ordovician, Richmond, of Colorado) are also referred to this group (Stensiö 1927, pp. 314—315; Bryant 1936; Moy-Thomas 1939, Berg 1940) but as very little indeed is known of their organization, it seems most appropriate not to assign to them any definite place in the system.

vertebrates is not proven, much less their affinities to the Heterostraci proper (Stetson 1928; 1931; White 1935a, pp. 435—436; Parker & Haswell 1940, p. 133; Romer 1945, p. 34; Balabaj 1948); possibly the group is heterogenous and polyphyletic, consisting of widely separated forms (Obruchev 1945, pp. 268—269; Westoll 1945, pp. 345—348; Balabaj 1948; Ørvig 1951, pp. 383,385, cf. also Gross 1947, pp. 110—111, Bystrov 1949). For the time being the only proper procedure is to regard the Thelodonti as a group with ambiguous content and unsettled affinities, and place them as *incertae sedis.*

The Heterostraci, after the exclusion of the Thelodonti, seem to form a natural group (White 1935a, p. 436). Our knowledge of the structure of these animals is derived mainly from the shape and composition of the exoskeletal plates and scales only, and owing to the fact that the endoskeleton is not at all ossified or only so in its superficial parts (the basal parts of the basal layer in the carapace, Stensiö 1927, p. 322) the fossils do not, as the Osteostraci, reveal much of the internal structures. In certain forms (particularly the Poraspids) the carapace reached rather far inwards so that some of the inner organs produced impressions on the inner side of the carapace (both the dorsal and ventral shields), and we have thus also here some clues towards an understanding of the organization of these animals. There are, however, still many obscure points to be made clear before we can wholly understand the structural plan of the group, its affinities to other groups, and its proper place in the system.

We shall here only dwell somewhat upon the impressions in the carapace produced by various internal structures, and their significance (cf. Lankester 1868, pl. 2:11; Kunth 1872, pl. 1:1,4-6; Alth 1874, pl. 5:1-2; Woodward 1891, pl. 9:4; 1898, fig. 2; pp. 4—5; Kemna 1903, fig. 5; pp. 355—358; Leriche 1906, figs. 5—7; pl. 1:2-5; pp. 22, 25—26; Jaekel 1927, fig. 5; pp. 178—180; Bryant 1926, pls. 1:1; 3:1-2; pp. 262—263; 1935, fig. 1; pls. 2, 5; pp. 115—116; Stensiö 1927, fig, 87; pp. 316—317, 323—326; Kiær 1930, figs. 1—3; 1932a, fig. 2; pls. 3:3; 6:1; Zych 1931, figs. 20—21, etc.; Kiær & Heintz 1935, figs. 3, 13, 36—38, many of the plates; White 1935b, fig. 3; Wills 1935, figs. 2—3; pls. 1:3-4,6; 3:5; Moy-Thomas 1939, fig. 1A; pp. 7—8; etc.).

Two generally large impressions in the foremost part of the dorsal shield, just behind the rostral margin, are interpreted as impressions of the paired nasal sac. There are no openings in the shield for the external nasal ducts, but a notch on each side of the carapace, on the incurved rostral margin of the dorsal shield or the postero-ventral margin of the rostral plate, is caused most probably by the nasal duct (Kemna 1904, p. 20; figs. 3—4, cf. Lankester 1870a, pl. 7:11-12; Bryant 1926, p. 262; Zych 1931, pp. 36—37, 42—43; photographs

6—9, 20; Kiær & Heintz 1935, p. 69; pl. 26). An indistinct groove backwards from each nasal impression in a *Poraspis* specimen is by Kiær & Heintz (1935, p. 90; pl. 26:2) regarded as having lodged the "olfactory lobe". In an *Anglaspis* specimen I have observed a distinct groove running from the impression of the (left) nasal sac in postero-median direction to the antero-lateral side of the pineal impression, and this groove I interpret as the groove for the n. olfactorius (or the tractus olfactorius). In the Heterostraci the olfactory organ must then have been a distinctly paired structure with paired, wholly separated external ducts which opened independently into the anterior part of the mouth cavity. Its relation to the hypophysis is unknown (the picture of the soft tissues in the anterior part of the head given by Stensiö 1932, pp. 185—191, is wholly fictitious; cf. Allis 1931b, pp. 70—71).

Of the median unpaired impressions we may note the pineal impression, produced by the pineal organ or, probably, by this organ and the saccus dorsalis (cf. Kiær & Heintz 1935, pl. 30:3). Behind the pineal impression is seen the impression caused by the mesencephalon, and it is in some cases provided with a slight median prominence often so shaped that a pair of small pits near the median line is formed (cf. Zych 1931, photograph 3; Kiær 1932a, pl. 6:1; Kiær & Heintz 1935, pl. 11; Wills 1935, fig. 2B; also observed by me in an *Anglaspis* specimen). The small pits are suggested to have been caused by the ductus endolymphatici (Wills 1935, p. 433) but this seems highly improbable, and I think it more likely that the prominence and the paired pits were caused by the roof of the mesencephalon being membranous (leading in to the ventriculus mesencephali) or by ridges in the brain roof corresponding to the eminentia tecti in *Petromyzon,* or probably to both these structures (cf. Ahlborn 1883, figs. 1, 5, 7; Bütschli 1912, fig. 404; Saito 1930, pl. 9; etc.). The impression caused by the medulla oblongata is often well developed and sometimes provided with a low rhomboidal prominence (cf. Zych 1931, photographs 1, 3; p. 42; Kiær 1932a, pl. 6:1; Kiær & Heintz 1935, pl. 30:3) which agreed in position to the fossa rhomboidalis of the medulla oblongata (Zych 1931, p. 42). Its posterior angle corresponded to the calamus scriptorius (which marks the boundary between the brain and the medulla spinalis). The part of the impression behind this point was thus caused by the spinal cord and not by the medulla oblongata (cf. White 1935b, fig. 3).

The V-shaped impressions produced by the anterior and posterior semicircular canals of the labyrinth organ are often well displayed, and it is to be noted that the impressions of some of the branchial pouches lay so closely to these former that there was no space left for a horizontal semicircular canal, and it is thus wholly evident that these animals possessed only the two vertical semicircular canals.

Very narrow grooves on the inner side of the dorsal and ventral shields just beneath and following the course of the sensory line canals (Kiær & Heintz 1935, pp. 70—71, 131) may have been caused by the lateralis nerves. It can in this connection only be noted that the pineal canal must have been innervated by a branch of the n. lateralis anterior (Stensiö 1926, p. 10), corresponding to the r. ophthalmicus in fishes.

The transverse impressions of the branchial pouches are generally six to eight in number on each side of the dorsal shield, and are often present also on the inner side of the ventral shield but are here less numerous than in the dorsal shield; in the ventral shield they are usually larger and broader than in the dorsal shield. The branchial impressions in the dorsal shield are present in two series on each side of the median line: the branchial impressions proper and the marginal branchial impressions. Each of the latter does not as a rule lie on the same transverse level as the corresponding impression on the disc but somewhat behind this level; they are, in some cases, forked, or subdivided into two pits (Jaekel 1927, fig. 5; Kiær 1932a, pl. 6:1; Kiær & Heintz 1935, pls. 11; 26:2; etc.). They are said by Zych (1931, p. 28) to join a longitudinal marginal "canal" which terminates at the branchial sinus in the dorsal shield. As pointed out by Kiær & Heintz (1935, p. 70; cf. pl. 11) the face of the branchial impressions often is not smooth but in some cases traversed by longitudinal (parallel to the main axis of the shield) grooves (cf. *Cephalaspis signata,* p. 135); pls. 27:2; 29:2). The branchial impressions on the disc have long been interpreted as impressions, produced by the gill-sacs; the marginal branchial impressions have been regarded as representing the openings of the gill-sacs into a common branchial duct (Bryant 1926, p. 263; cf. Moy-Thomas 1939, fig. 1A), or "the ducts leading from the pouches into the common external branchial opening" (Wills 1935, p. 433), or into a common external duct (Zych 1931, p. 29). It seems, however, not very probable that these impressions are due to the ducts themselves but rather to some structures in the dorsal wall of the ducts or in the lateral parts of the gill-sacs proper, and we can in this connection remember the thymus-like organs which are present in *Petromyzon,* a pair dorsally to each external branchial duct (Schaffer 1894; Castellaneta 1913; Salkind 1915).

On the inner side of the ventral shield we find in some cases a pair of generally rounded pit-like impressions near the median line in front of the branchial impressions, and behind them a paired groove is seen in some specimens. The anterior part of this groove lies transversally in front of the median half of the first branchial impressions, and passes rather abruptly over into the posterior longitudinal part;

this part of the groove farther backwards joins its fellow of the opposite side and an unpaired median groove is thus formed ending posteriorly rather suddenly (Kiær & Heintz 1935, figs. 3, 13; pls. 12:2-3; 26:3; 27:2). The interpretation of these structures is uncertain; the grooves are possibly impressions of vessels (cf. Wills 1935, p. 434), the truncus arteriosus or a v. jugularis inferior, comparable to that in *Petromyzon,* but this does not seem to be a satisfactory interpretation; perhaps more likely, they are impressions of the endostyle and the postero-ventral parts of the peripharyngeal grooves (cf. the corresponding structures in the Cephalochordata: Müller 1873; Dohrn 1885; Lankester 1889, pp. 386—388; Willey 1894, pp. 31—32, 34, 140, 167—169; Franz 1927, pp. 541—547; Drach 1948, p. 951; etc., in *Petromyzon:* Schneider 1879; Dohrn 1885; Gaskell 1899; Reese 1902; Kieckebusch 1928; Leach 1939; etc. and in *Eptatretus:* Stockard 1906, cf. Brachet 1935, p. 488). The nature of the paired pits before the grooves is wholly obscure.

We can furthermore mention that the eyes lay laterally, in a notch or an opening in the dorsal shield, or in an opening in a separate orbital plate, and that the mouth formed a subterminal, or ventral transverse slit, strengthened by a mouth skeleton, consisting ventrally of independent exoskeletal oral plates and postoral covers, and dorsally of a transformed part of the dorsal shield or of the rostral plate ("the maxillar brim" or "the maxillary tooth-plate", Kiær 1928, cf. Stensiö 1932, pp. 183—185; Kiær & Heintz 1935, p. 44; White 1935a, pp. 408—412).

A morphologically most important characteristic in the organization of the Heterostraci was the presence of a paired olfactory organ (with independent external ducts), situated near the anterior end of the head, revealing that the rostral part of the head was formed by the ethmoidal region (Stensiö 1927, p. 323). Following Kiær (1924, p. 121; cf. Säve-Söderbergh 1941a, p. 537, foot-note 2; Balabaj 1948) I regard this feature as of fundamental significance, even if it cannot be used (as by Kiær) as a primary factor for the separation of all the vertebrates into two distinct main groups. However, it distinguishes the Heterostraci from the Osteostraci and Anaspida as well as from the recent Cyclostomes (both the Petromyzonts and the Myxinids), and it signifies that the group cannot, contrary to Stensiö (1927), be regarded as more closely allied to the Myxinids than to other agnathous groups (cf. Derjugin 1928; Goodrich 1931, de Beer 1931; Sewertzoff 1931, pp. 58—61; White 1935a, pp. 429—435; Moy-Thomas 1939, pp. 24—26; Säve-Söderbergh 1941a, p. 537, foot-note 2; Obruchev 1945, p. 271; Romer 1945, p. 33; Balabaj 1948).

In the ontogenetic development of the olfactory organ the Cyclostomes and the Gnathostomes represent two distinct types (cf. Peter

1901; 1911; Matthes 1934, pp. 883—886; Brachet 1935, pp. 449—458; etc.) in so far as in the former group the organ arises from an unpaired median placode ("placode olfacto-hypophysaire", Brachet) while in the latter group there is a pair of distinctly separated olfactory placodes without connection with any of the hypophyseal rudiments. The Cyclostome type is, however, generally regarded to be aberrant and not to represent primitive conditions (cf. also Bütschli 1921, p. 707).

The impressions of the gill-apparatus indicate that the gills were built essentially as in the Cyclostomes (cf. e. g. Kemna 1903, pp. 355—358; Stensiö 1927, p. 325). The external ducts from each gill-sac very probably joined to form a common efferent duct, but the agreement in this respect between the Heterostraci and *Myxine* (Stensiö 1927, p. 326) is certainly superficial and without any significance (Sewertzoff 1931, p. 59, foot-note; Rauther 1937c, p. 224; Balabaj 1948). Franz (1927, pp. 628—629; 1937, p. 15), however, regards the common efferent branchial duct in *Myxine* (and furthermore also the independent external ducts in *Eptatretus* and in *Petromyzon)* as a remnant of the peribranchial chamber in the Cephalochordata, but this view is unique, and the conditions in *Myxine* are generally regarded as secondary (Goodrich 1930, pp. 493—494). Whether the common efferent duct in the Heterostraci really was such a rest of the peribranchial chamber, inherited from their pre-vertebrate ancestors, or not, can of course not be decided.

The presence in the labyrinth organ of the Heterostraci of only the two vertical semicircular canals is distinctly a Cyclostome characteristic (the labyrinth of the Myxinids, with seemingly only one semicircular canal but with two ampullae, is principally built as in the Petromyzonts, Burlet 1934, p. 1303).

If the median impressions on the ventral side of the dorsal shield reflect the main features of the brain, and they apparently do so, then we can infer that a cerebellum was not (or at most very feebly) developed (Kiær & Heintz 1935, p. 70), and furthermore that the mesencephalon was provided with a plexus chorioideus. Now we find that the cerebellum in the recent Cyclostomes is very small (Petromyzonts, cf. Johnston 1902; Stefanelli 1939; Larsell 1947, pp. 406—440; Heier 1948) or absent externally (Myxinids, Larsell 1947, pp. 398—406), and that the plexus mesencephali, contrary to the conditions of all other vertebrates, is present in the Petromyzonts (Bütschli 1912, pp. 566—567).

From what is known or assumed with regard to the organization of the Heterostraci we can deduce that they must have been agnathous vertebrates with distinct cyclostomous characteristics but at the same time in some important traits (the formation of the rostral part of the head and the paired olfactory organ) differing markedly from the Cyclostomes (as well as from the Osteostraci and the Anaspida). It is thus most consistent to follow those authors who regard the Heterostraci as a separate group of the Agnatha, not closely akin to the other agnathous groups (Kiær 1932a; Säve-Söderbergh 1941a; Obruchev 1945; Romer 1933; 1945; Balabaj 1948); possibly the group was allied to the basal stock from which both the other agnathous groups and the Gnathostomes evolved (Romer; Säve-Söderbergh).

The real nature of the very enigmatic fossil *Jamoytius* (White 1946b; cf. Drach 1948, p. 1035; Oakley & Muir-Wood, 1948, fig. on p. 16) is obscure. It is by White regarded as representing a new order (Euphanerida) of primitive agnathous vertebrates which is thought to have formed the ancestral stock of all vertebrates (Agnatha as well as Gnathostomata). Not very much is known of its organization (the remains interpreted as those of the notochord seem to be very ambiguous). It can, however, be mentioned that the position of the eyes near the anterior end of the head indicates that the rostral part of the head was not formed as in the monorhinous Agnatha but rather as in the Heterostraci and the Gnathostomata. Although the absence of any vestiges of gill-openings can possibly be explained by the state of preservation of the fossil (White 1946b, p. 93), it can, on the other side, reflect a structural characteristic of the animal in so far as there was possibly only one external opening (atrioporus?) not likely to be preserved (cf. also the conditions in the Thelodonti, see e. g. Kiær 1932b, p. 8). The possibility that *Jamoytius* was a larval or naked form belonging to the Thelodonti does not seem wholly excluded.

The small, Mesodevonian, cyclostome-like *Palaeospondylus,* which has played such an important role in the discussions on the ancestry and the evolution of the Cyclostomes is now generally regarded as a Gnathostome (cf. Derjugin 1928; Moy-Thomas 1940; Parker & Haswell 1940, pp. 169—172; Romer 1945, pp. 57—59; 1946, p. 55).

With regard to the relations between the Osteostraci and the modern Cyclostomes, it is apparent from the preceding chapters on the anatomy of the Osteostraci that the inner structures of these fossils can be explained by comparisons with the inner anatomy of the Cyclostomes (mainly *Petromyzon* and particularly its larval form, Ammocoetes). This fact indisputably supports the view that real, profound and important conformities exist in the organization between the Osteostraci and the Cyclostomes. It has also been shown that these resemblances are considerably greater than assumed by Stensiö (1927, 1932), and that the organization of the Osteostraci (particularly with regard to the composition of the anterior visceral parts of the head) is not in any way fundamentally different from that of the Cyclostomes (cf. Damas 1943, pp. 232—233, 267). The fact that the Osteostraci have more points in common with the Petromyzonts (Ammocoetes) than with the Myxinids cannot be taken as evidence that they are more closely related to the former than to the latter group but only that the Ammocoetes still possesses many primitive features which are lost in the adult Petromyzonts and in even higher degree in the Myxinids. Despite all dissimilarities it must be assumed that the recent cyclostomous groups are related and form a monophyletic branch of the Agnatha in which the Myxinids in many respect representent a highly specialized and transformed group.

In conclusion we can say that the Osteostraci form an independent group of the monorhinous, agnathous vertebrates, on a par with the groups Anaspida and Cyclostomata, with which they thus are more closely akin than with the diplorhinous Heterostraci.

The position of the Osteostraci in the vertebrate system can be expressed in the following arrangement (which most closely agrees with that of Kiær & Heintz 1935; cf. also Obruchev 1945):

VERTEBRATA
A. Agnatha
    1. Diplorhina (Pteraspidomorphi)
    2. Monorhina (Cephalaspidomorphi)
        Osteostraci (Cephalaspida)
        Anaspida
        Cyclostomata
B. Gnathostomata.

Stratigraphical remarks.

The cephalaspid-bearing strata in Spitsbergen. — The Devonian deposits in Spitsbergen are exposed in two different areas, viz. a small area on both sides of the Hornsund Bay in S. Spitsbergen, and a much larger one in N.W. Spitsbergen. Only this latter area is here of interest. It extends from the North coast to the inner parts of Bille Bay, Dickson Bay and Ekman Bay in the Ice Fiord, and from Wijde Bay in the east to a line running south from Red Bay in the west, with offshoots farther west to Kings Bay (fig. 1). The main field is limited to the east and west by north-south running fault-lines, and forms a large, down-faulted area (Nathorst 1894). In the W. part of this complex there is a second long north-south fault-line, dividing the main area into two blocks; the W. block is tipped to the west and a long range of the underlying Caledonian rocks is exposed along the E. part of this block (Holtedahl 1914a; 1914b; Føyn & Heintz 1943). For further information on the deposits and the distribution of the different subdivisions, mentioned below, the reader is referred to the important paper by Føyn & Heintz (1943), in which also the older literature is cited.

The Devonian system in N. Spitsbergen was divided into four series by Hoel and Holtedahl (Hoel 1914; Holtedahl 1914a; 1914b) who based their divisions on studies in the field and on preliminary determinations of the fossils by Kiær (see Kiær 1916). The four series are:

4. Wijde Bay series,
3. Grey Hoek series,
2. Wood Bay series,
1. Red Bay series.

The layers in the four series rest conformably upon each other in some places, and there is apparently no break at all, or none of considerable magnitude, in the sedimentation of the deposits between the different series.

The Wijde Bay series contains no Cephalaspids, and it is not further discussed here; its age is Upper Mesodevonian (see Heintz 1937; Nilsson 1941; Høeg 1942; Føyn & Heintz 1943).

The most detailed consideration of the stratigraphy of the Red Bay series is that by Heintz (in Kiær & Heintz 1935), and, as indicated by him, this is only a preliminary survey, and is, in fact only a short enumeration and tabulation of the different fossiliferous "horizons" or localities in the Fraenkel Ridge and Mt Ben Nevis on the E. side of Red Bay. We cannot, however, obtain as yet a clear picture of the geology of these mountains; the interrelations of the different layers and what is meant by the horizons discerned are often quite obscure. After Kiær (1932a; see Føyn & Heintz 1943, p. 42) the series can be divided into two parts, a lower one, the Fraenkel Ridge division, and an upper one, the Ben Nevis division.

In the Fraenkel Ridge division, fossils have been collected in several localities on the Fraenkel Ridge, and these localities have been grouped into six different horizons (Kiær & Heintz 1935, pp. 12—13), viz. (from the lowest to the uppermost): 1. the "Psammosteus" horizon; 2. the Corvaspis horizon; 3. the Plant horizon; 4. the Primaeva horizon; 5. the Polaris horizon; 6. the Anglaspis horizon.

The strata of the Ben Nevis division which very probably form a direct continuation upwards of those in the Fraenkel Ridge division have been more closely studied by Hoel in 1909—1910, who measured twenty fossiliferous horizons in two different, widely separated profiles (see Kiær & Heintz 1935, pp. 14—16). New localities were discovered during Vogt's expeditions in 1925 and 1928, and their place in the stratigraphical table is more or less positively indicated by Heintz (Kiær & Heintz 1935, pp. 14—16). In 1939 fossils were collected without attention being paid to the stratigraphical position of the localities. In the following the different localities in Mt Ben Nevis with specifically determinated Cephalaspids are arranged into four groups, the relative stratigraphical position of which seems to be fairly certain, except that I am not quite convinced that the Vogti horizon is situated above the horizons A—I: 1. the lowermost group, comprising the horizons A—I of Hoel; 2. the Vogti horizon; 3. the Ctenaspis horizon (corresponding approximately to the horizons J—L of Hoel); 4. the Benneviaspis horizon (corresponding approximately to the horizons O—R of Hoel).

The stratigraphy of the Wood Bay series and the Grey Hoek series (as well as the Wijde Bay series) have been studied particularly during the ENS Spitsbergen expedition in 1939 (Føyn & Heintz 1943) but (as pointed out by the authors) the geological investigation was of "a more or less casual character" and the results "cannot be regarded as an exhaustive description of the geological conditions" (Føyn & Heintz 1943, p. 9).

The Wood Bay series was divided into three divisions: (from the oldest to the youngest) 1. the C. Kjeldsen division ("Kapp Kjeldsen division"); 2. the Lyktan ("Lykta") division; 3. the Stjørdalen division (Føyn & Heintz 1943, p. 13). The three divisions are characterized by their petrological composition and by index-fossils (mainly genera

Table 1. The distribution of Cephalaspids in the different parts of the Red Bay series in Spitsbergen.

	Fraenkel Ridge						Mt Ben Nevis				
	"Psammosteus" horizon	Corvaspis horizon	Plant horizon	Primaeva horizon	Polaris horizon	Anglaspis horizon	Horizons A—I	Vogti horizon	Ctenaspis horizon	Benneviaspis horizon	Mt Petraspis
Cephalaspis corystis	×										
„ *acuminata*		×		×		?					
„ *dissimulata*		×		×	×	×					
„ *cradleyensis*			×								
„ *pygmaea*			×	×							
„ *hyperboreus*				×							
Ectinaspis heintzi				×							
Cephalaspis oreas				×	?						
„ *divaricata*				×		?					
„ *eurhynchus*				×		?					
„ *verruculosa*				×		?					
„ *heintzi*				×		×					
„ *sinuata*				×		×					×
„ *arcticus*					×						
„ *deltoides*						×					×
„ *eurynotus*						×					
„ *excellens*						×					×
„ *hastata*						×					
„ *powriei* var.						×					
„ *recticornis*						×					×
„ *vogti*						×					×
„ *exilis*							×		×	×	
Securiaspis staxrudi							×			×	
Tegaspis kolleri							×			×	
Cephalaspis føyni								×			
„ *ibex*								×			
Benneviaspis longicornis								×			
Cephalaspis doryphorus									×		
„ *hoeli*									×	×	
„ *platycephalus*									×	×	
„ *retusa*									×	×	
Benneviaspis holtedahli									×	×	
Hoelaspis angulata									×	×	
Kiaeraspis auchenaspidoides									×	×	
Benneviaspis platessa									?	×	
Cephalaspis eukeraspidoides										×	
„ *metopias*										×	

Table 2. The distribution of Cephalaspids in the different parts of the Wood Bay series in Spitsbergen.

	C. Kjeldsen div. upper part	C. Kjeldsen div. lower part	Lyktan div.	Stjørdalen div.
Benneviaspis grandis	×			
„ *lövgreeni*	×			
„ *maxima*	×			
Boreaspis batoides	×			
„ *ceratops*	×			
„ *rostrata*	×			
Cephalaspis isachseni	×			
„ *jarviki*	×			
„ *watneliei*	×			
„ *brevicornis*	?			
Boreaspis puella	×	?		
Cephalaspis producta	×		?	
„ *curta*	×			?
„ *caroli*	×	×		
„ *fracticornis*	×	×		
„ *laticornis*	×	×		
Boreaspis intermedia	×	×		
„ *macrorhynchus*	×	×		
Axinaspis whitei	×	×		
Cephalaspis oblonga	?	×		
Boreaspis costata	?		×	
Acrotomaspis instabilis		×		
Nectaspis peltata		×		
Boreaspis circinus		×		
„ *spinicornis*		×		
„ *triangularis*		×		
„ *gracilis*		×	×	
„ *robusta*		×	×	
„ *curtirostris*			×	
Cephalaspis høegi			×	
„ *lanternaria*			×	
„ *menoides*			×	
Acrotomaspis sp. 1			×	
Nectaspis areolata			×	×
„ *dellei*				×
Cephalaspis moy-thomasi				×
„ *semicircularis*				×
Acrotomaspis trinodis				?

of Pteraspids and Placoderms). At least in one locality (S.W. part of Mt Sigurd) the C. Kjeldsen division was found resting conformably upon the Red Bay series.

The vertical distribution of the Cephalaspids in Spitsbergen. — We may now consider in some detail the distribution of the Cephalaspids in the different strata of the Spitsbergen Old Red.

Cephalaspids are known to occur from the lowermost fossiliferous horizon in the Red Bay series up to the Grey Hoek series, inclusive; they are common in the whole Red Bay series and in the two lower divisions of the Wood Bay series but are much rarer in the upper division of this series and in the Grey Hoek series.

From the Grey Hoek series only a fragment of a *Cephalaspis?* sp. (p. 424) and an indeterminable specimen of the genus *Acrotomaspis* (p. 536) is known.

The distribution of the Cephalaspids in the different parts of the Red Bay and the Wood Bay series is shown in the two tables (1, 2) above. An interrogation mark in the tables indicates that the specific determination of the fossil in the horizon (or the division) is uncertain. It must be noted, that the horizons cited in the columns for the Ben Nevis division do not cover the whole sequence of strata in this division; there are fossiliferous horizons both below the horizon A and above the Benneviaspis horizon; they are not included here since they do not contain any specifically determinable cephalaspid forms.

As is seen from the tables, the distribution of the Cephalaspids in the different parts of the series is rather uneven. The fact that the Stjørdalen division is poorer in species (and individuals) than the two other divisions of the Wood Bay series possibly reflects the real conditions that the Cephalaspids become rarer higher up in the series. In the Red Bay series, where some of the horizons contain a few species only, this fact is, however, to some extent to be explained by lack of uniformity during investigation; thus, in 1939, collections were made principally in the Primaeva and Anglaspis horizons of the lower division. It is, furthermore, to be noted, that the tables do not of course register the whole cephalaspid fauna; in almost every horizon or division there are found indeterminable cephalaspid fragments which, as a rule, cannot be further considered here. This calls for caution in the comparison between the faunas in different horizons.

C. apicalis, C. lata, and *C. spitsbergensis,* as being dubious species, are not included in the tables.

The Red Bay series is characterized by a large number of *Cephalaspis* species, often of a distinct type, different from the general type of the species in the overlying Wood Bay series; they have generally a rather narrow cephalic shield, narrow pectoral sinus, short or long but never very broad cornua. The series contains furthermore some cephalaspid genera, not found in the Wood Bay series, viz. *Ectinaspis, Securiaspis, Tegaspis, Hoelaspis,* and *Kiaeraspis,* but none of them can be used as index-fossil for the whole series. *Benneviaspis* is also found here with several, apparently rather unspecialized forms which are quite different from those in the lowermost part of the Wood Bay series.

The different horizons of the Fraenkel Ridge division have no cephalaspid form in common which can serve as a guide fossil for the whole division. It is distinguished by several species of *Cephalaspis* (see table 1), not occurring higher up in the series, and by the genus *Ectinaspis* (known, however, only from one locality). Otherwise, in relation to the Ben Nevis division, it is negatively characterized by the absence of most of the genera of this division.

It will be noted that in the lowermost fossiliferous horizon, the "Psammosteus" horizon, beside *C. corystis,* an indeterminable *Cephalaspis specimen* (p. 426) is also found.

The cephalaspid faunas in the Corvaspis, the Plant, the Primaeva, and the Polaris horizons do not (with our present knowledge) seem to be very different from each other; the Corvaspis horizon contains no species of its own, the Plant horizon and the Polaris horizon each one only. The Primaeva and the Anglaspis horizons, which both are rather well known and rich in fossils, can better be compared. While there is a (probably considerable) number of species that are common to both horizons, there appear in the Anglaspis horizon many new species, characterizing this layer, and the two horizons seem thus to be well separated, and may represent two different zones (or sub-zones).

The Ben Nevis division is well characterized by several *Cephalaspis* species of its own (see table 1), some of them, as *C. exilis,* occurring in a major part of the division, and furthermore by a number of distinct genera, *Securiaspis* and *Tegaspis* in a large part of the division, *Hoelaspis* and *Kiaeraspis* in the upper part of the division, and finally by some *Benneviaspis* species (the genus is found in almost the whole division[1] but continues also up into the Wood Bay series).

No species are with certainty known to occur in both the Fraenkel Ridge and the Ben Nevis divisions; a specimen, doubtfully placed in *C. hastata* (a species known from the Anglaspis horizon) is, however, found on Mt Ben Nevis and thus in the upper part of the series (it can furthermore be noted that *C. hastata* is very

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[1] It can in this connection be noted that a specimen, somewhat doubtfully assigned to *B. holtedahli,* is found in the lowermost part of the division, distinctly below the horizon A or the Vogti horizon (p. 454; ENS no. 614), and furthermore that an undetermined specimen (mentioned on p. 448) comes from the horizon T, thus from a layer above the Benneviaspis horizon.

similar, and probably very closely related to *C. ibex* from the Vogti horizon).

The following species are found in localities which beyond doubt belong stratigraphically to the Ben Nevis division but the exact place of which in the series is unknown, viz. *C. aarhusi, C. broughi, C. crofti, C. gracilis, C. hastata?, C? pedata, C. pinnifera, C. signata, C. tenuicornis, Securiaspis quadrata, Securiaspis* sp., *Benneviaspis* sp. 1.

The different parts of the Ben Nevis division cannot be properly compared since only a few species are known from the lower part of the series as against a rather rich fauna in the upper part. We can note that the three species in the Vogti horizon are restricted to this layer while the three species in the group, comprising the horizons A—I, are also known from the upper part of the series; more exactly, *C. exilis* is found in horizon A as well as in the Ctenaspis and the Benneviaspis horizons, *Securiaspis staxrudi* occurs in the horizon H (a specimen from horizon G is hesitatingly placed in this species) and in the Benneviaspis horizon, and *Tegaspis kolleri* in horizon F or G and in the Benneviaspis horizon. The upper parts of the division, the Ctenaspis and the Benneviaspis horizons, which can hardly be separated faunistically from each other, are characterized by a number of species of their own and especially by the genera *Hoelaspis* and *Kiaeraspis* which here occur for the first time (being absent from the lower parts of the division).

From the table 1 is seen that several species from the Fraenkel Ridge division (the Primaeva and the Anglaspis horizons) are found also on Mt Pteraspis, and from this we can infer that the layers in Mt Pteraspis can be assigned at least partly to the upper part of the Fraenkel Ridge division (cf. Kiær & Heintz 1935, p. 15). An upper part of the strata in Mt Pteraspis has previously been correlated tentatively with a part of the Ben Nevis division (Kiær & Heintz 1935, pp. 15—16); the older view that the layers in Mt Pteraspis constitute the uppermost parts of the Red Bay series (Kiær 1916, p. 492; see e. g. the table in Quenstedt 1926, p. 6) is undoubtedly wrong.

Hoelaspis angulata, known from the Ctenaspis and the Benneviaspis horizons on Mt Ben Nevis, is found also in the S.W. part of Mt Sigurd, in the uppermost part of the Red Bay series, not far below the boundary towards the Wood Bay series.

If we now turn to the distribution of the Cephalaspids in the Wood Bay series, we find first of all a fauna, quite different from that of the Red Bay series. The genera *Cephalaspis* and *Benneviaspis* are the only genera common to the two series, no species being common to them.

The genus *Cephalaspis* is represented in the Wood Bay series (see table 2) by many species but they are generally of a type different from that of the species in the Red Bay series, having large, very broad and flattened cephalic shields, strongly developed, broad cornua, wide pectoral sinus and often narrow inter-zonal parts, the lateral sensory fields are often remarkably narrow, lying near the lateral margins of the shield *(C. pinnifera* from the upper Red Bay series is of about the same type), and there is generally no close affinity between the species from the two series. Also the species of *Benneviaspis* are partly morphologically different from those in the Red Bay series. The genera *Hoelaspis, Kiaeraspis, Tegaspis,* and *Securiaspis* do not continue upwards into this series. On the other hand, some new genera appear now for the first time, viz. *Boreaspis* (closely related to *Hoelaspis), Axinaspis* and *Acrotomaspis* (both related to *Kiaeraspis),* and *Nectaspis;* none of these genera is, however, found through the whole series, although *Nectaspis* and *Acrotomaspis* are absent only from its lowermost part.

Of the species, mentioned in table 2, some are also found in localities, the exact position of which in the series is uncertain: *Boreaspis spinicornis* known with certainty from the upper part of the C. Kjeldsen division is also found in talus on the S. W. slope of Mt Lyktan; the transition between the C. Kjeldsen division and the Lyktan division lies probably near the base of the mountain (see Føyn & Heintz 1943, p. 38). A specimen of *B. costata* is found in the shore profile below Mt Lyktan, and it is therefore possible that it comes from the uppermost fart of the C. Kjeldsen division. *B. robusta* (from the upper part of the C. Kjeldsen division and the Lyktan division) and *Nectaspis dellei* (from the Stjørdalen division) are found also in localities which may belong to either the Lyktan or the Stjørdalen division. *Acrotomaspis trinodis* is also found in similar localities; some specimens, doubtfully placed in this species, come from a locality unquestionably in the Stjørdalen division.

The table over the distribution of the Cephalaspids in the Wood Bay series must be used with caution as it is often difficult to decide whether a species is restricted to a certain division (or part of a division) or not.

The type specimen of *C. brevicornis* comes most probably from the Wood Bay series; from the same series but from an undetermined division are *C. borealis* and *C. acuticornis. C. gigas* comes from a not specified part of the C. Kjeldsen division, and some doubtfully determinated specimens of the same species from the Lyktan division. An undetermined *Benneviaspis* specimen *(B.* sp. 2, p. 466) is found in the upper parts of the Wood Bay series, either in the Lyktan or in the Stjørdalen division.

The different divisions of the Wood Bay series, distinguished by Føyn & Heintz (1943), are each more or less well characterized by its cephalaspid fauna.

The C. Kjeldsen division contains a large number of species of *Cephalaspis, Benneviaspis,* and *Boreaspis* which are peculiar for the division, as is also the genus *Axinaspis;* in the upper part of the division the genera *Acrotomaspis* and *Nectaspis* appear, but they are present also in the other divisions of the series.

In table 2 the C. Kjeldsen division has been divided into two parts, a lower one found in Mt Sigurd, and an upper one, and the species from each part are tabulated separately. From the table is seen that these parts are as well characterized by peculiar cephalaspid species as are the other divisions of the series. Føyn & Heintz (1943, p. 20) have also suggested that the lowermost part of the C. Kjeldsen division "may prove to be a separate sub-division". We can note the presence, exclusively in this part, of three *Benneviaspis* species, furthermore some *Cephalaspis* species (rather similar to the general *Cephalaspis* type in the Red Bay series), and three *Boreaspis* species, and finally the absence of the genera *Acrotomaspis* and *Nectaspis.*

The upper part of the C. Kjeldsen division has a number of species as well as the genus *Axinaspis* in common with the lower part but is, on the other hand, connected with the overlying divisions by the presence of the genera *Acrotomaspis* and *Nectaspis* (which besides in this part occur both in the Lyktan and the Stjørdalen divisions). Characteristic Cephalaspids for this upper part are certain species of *Boreaspis* and *Nectaspis* (see table 2).

The Lyktan division is distinguished by the presence of some characteristic species of *Cephalaspis* (see table 2) and one *Boreaspis* species *(B. curtirostris),* one (as yet unnamed) species of *Acrotomaspis,* and especially by the joint occurrence of the two common species, *Nectaspis areolata* and *Boreaspis robusta* (this latter species is, however, lacking in some areas, e. g. at Ekman Bay; *B. robusta* appears already in the upper part of the C. Kjeldsen division, and *N. areolata* continues upwards into the Stjørdalen division).

The topmost division of the Wood Bay series, the Stjørdalen division, is, as far as the cephalaspid fauna is concerned, not very well distinguished from the Lyktan division; it is negatively characterized by the decrease in number of the species and individuals of the Cephalaspids. Two *Cephalaspis* species *(C. moy-thomasi, C. semicircularis)* are peculiar for this division; *Nectaspis areolata* is still present but in company with another species of the same genus, *N. dellei;* the genus *Acrotomaspis* is also found here.

Correlation with other areas. — With regard to the relative age of the different Old Red series in Spitsbergen earlier authors held the view that the Red Bay series is Upper Silurian (Downtonian), the Wood Bay series Eodevonian, the Grey Hoek series

Mesodevonian, and the Wijde Bay series Neodevonian (see e. g. Holtedahl 1914a).

Kiær's position (which was a basis for the views of Hoel, 1914, and Holtedahl, 1914a, 1914b) as to the age of the Red Bay series is evident from his paper of 1916 (Kiær 1916). He regards the Red Bay series as of Upper Silurian, Downtonian, age, meaning here Downtonian in the common signification at that time, as the age of the layers which in England are situated between the Upper Ludlow beds and the Lower Old Red sandstone; he was i. a. of the opinion that Cephalaspids in the Red Bay series were most closely allied to the genera *Didymaspis, Sclerodus* and *Thyestes*. The Wood Bay series is in the same paper considered to be Eodevonian.

Later the extent of the Downtonian was somewhat widened by King (1921) to cover also a lower part of the Lower Old Red (finally, King 1934, p. 527, with ten different stages: I. 1—10) while an overlying part was separated under the name Dittonian (with the stages II. 1—4). King considered (1934, p. 553) both Downtonian and Dittonian to belong to the uppermost Silurian. Stamp (1923, p. 406) and King (1934, pp. 550, 553) referred an uppermost part of the Red Bay series in Spitsbergen to the Dittonian.

In a later paper Kiær (1931, pp. 425—426, 430) includes the Dittonian in the Downtonian as a part of this formation, and refers the whole series to the Lower Eodevonian (Gedinnian). In Spitsbergen the Red Bay series pertains here. The Wood Bay series is now regarded as "the upper part of the Lower Devonian in Old Red development corresponding to the marine Coblentzian" (Kiær 1931, p. 430).

Now some authors refer the whole Red Bay series to the Downtonian without explaining their conception of the term "Downtonian", as Quenstedt (1926, p. 6), Hoel (in Stensiö 1927, p. X), Frebold (1935, p. 21), Solle (1935, p. 52), while Heintz (in Kiær & Heintz 1935) probably follows the opinion of Kiær of 1931 (cf. Säve-Söderbergh 1937, p. 255; 1941b, pp. 238—239), and others (especially in later years) explicitly state that a lower part of the Red Bay series is Downtonian, an upper part Dittonian (besides Stamp and King, cited above, Säve-Söderbergh 1937, p. 255; 1941b, pp. 239—240; Heintz 1937, p. 21; Vogt 1938, p. 88; Høeg 1942, p. 162; Føyn & Heintz 1943, pp. 42—45; White 1950a, p. 64; 1950b, p. 86; Gross 1950, pp. 37—38). Some of these authors (Heintz, Høeg, Føyn & Heintz) regard the Dittonian as part of the Silurian, inasmuch as they speak of the (lower part of the) Wood Bay series as "Lower Lower Devonian", while Säve-Söderbergh draws the Silurian-Devonian boundary between the Downtonian and the Dittonian, and White (as earlier i. a. Stamp) includes the Downtonian in the Devonian as its lowermost part (this latter view is at present the most commonly accepted one, see e. g. the handbook of Kayser & Brinkmann 1948; the Gedinnian, which partly corresponds to the Downtonian, has long been considered as Eodevonian, cf. e. g. Asselberghs 1946).

In this connection, regarding the age of the Red Bay series, I shall refer briefly to the opinion of Säve-Söderbergh (1941b, pp. 239—240) as being the first well documented correlation of the fauna of the series in question and as based mainly on the character of the cephalaspid fauna. He emphasizes (on the basis of the stratigraphical survey by King of the Cephalaspids of Great Britain, in Stensiö 1932, pp. 199—204) i. a. the great resemblance in the cephalaspid fauna (with the genera *Cephalaspis, Securiaspis* and *Benneviaspis)* that exists between the Dittonian of England and the upper part of the Red Bay series. He thinks furthermore that only a lower part of the Fraenkel Ridge division is Downtonian while its upper part (on account of the supposed presence in this part of *Cephalaspis* species known from the Ben Nevis division) as well as the whole Ben Nevis division, (and the "Mt Pteraspis group" which erroneously is counted as a special uppermost division) is considered to be Dittonian. White (1950a, p. 64; 1950b, p. 86) is of about the same opinion (his conception as to the upper limit of the Downtonian is, however, somewhat dissentient, see further below), and Føyn & Heintz (1943, p. 44) evidently regard the whole Fraenkel Ridge division as Downtonian, the Ben Newis division as Dittonian.

With regard to its age the Wood Bay series is commonly regarded as Eodevonian (without more exact statement as to which part of this series is meant), so by Quenstedt (1926, p. 6), Hoel (in Stensiö 1927, p. X), Solle (1935, p. 52), Frebold (1935, p. 27), Schenk (1937, p. 121), as "Lower Lower Devonian" by Heintz (1929a, pp. 76, 78; = Siegenian, 1937, p. 17, cf. table), as Lower Eodevonian, possibly extending into the Upper Eodevonian, by Vogt (1938, p. 88). Føyn & Heintz (1943, pp. 45—48) think that only the lower division (the C. Kjeldsen division) of the series can be determined stratigraphically as "Lower Lower Devonian" while the question as to the age of the two upper divisions (the Lyktan and the Stjørdalen divisions) as well as that of the Grey Hoek series cannot at present be definitely settled. These divisions must, however, be placed between the "Lower Lower Devonian" and the Upper Mesodevonian which is the age of the conformably overlying Wijde Bay series. Høeg (1942, pp. 161—168) follows Føyn & Heintz but points out the remarkable fact that the fossil flora of the Wijde Bay series on the whole is quite distinctly of a Neodevonian type.

The Grey Hoek series is considered (with a varying conception as to the extent of the series) to be Uppermost Eodevonian or Lowermost Mesodevonian (Quenstedt 1926, p. 6; Hoel, in Stensiö 1927,

p. X; Frebold 1935, p. 27), possibly "Middle Lower Devonian" to "Lower Middle Devonian" (Heintz 1929a, p. 78), Mesodevonian (Solle 1935, p. 52; Schenk 1937, p. 121, who wrongly regarded the Grey Hoek series as younger than the Wijde Bay series, cf. Heintz 1937, p. 20, Føyn & Heintz 1943, p. 35).

We shall now examine if our extended knowledge of the cephalaspid fauna of Spitsbergen has any bearing upon the question of the age of the different series in the Spitsbergen Old Red. Before that we must, however, define some stratigraphical terms, used here. The meanings of these terms which are taken from the type profiles of the Eodevonian in England, the Ardennes and the Rhineland are evident from the following generalized and simplified table:

Mesodevonian (Middle Devonian)		Couvinian (Eifelian s. 1.)
Eodevonian (Lower Devonian)	Upper	Emsian (Coblentzian; Upper Coblentzian)
		Siegenian (Lower Coblentzian)
	Lower	Dittonian (Upper Gedinnian)
		Downtonian (Lower Gedinnian)
Silurian		Upper Ludlow group

As to the boundary between the Downtonian and Dittonian, I follow White (1950a; 1950b) who places it at the base of the zone with *Pteraspis leathensis* and at the top of the zone with *Traquairaspis symondsi* (corresponding approximately to the stages I.9 and I.8 of King, respectively, cf. King 1934, p. 527) and thus somewhat lower than King. The base of King's Dittonian is at a level which in White's stratigraphical column belongs to the following zone, that of *Pteraspis crouchi.* This zone is the upper one of the two zones recognized by White in the Dittonian, and the Siegenian begins with the appearance of large *Pteraspis* species of the subgenus *Archaeoteuthis (= Rhinopteraspis),* here, more specifically, *P. (A.) dunensis.*

The Red Bay series. As White considers the replacement of *Traquairaspis* by *Pteraspis* in England as a most noteworthy change in the fauna, it is natural that he (White 1950b, p. 85) also places the Downtonian-Dittonian boundary in Spitsbergen somewhere between the "Psammosteus" horizon, in which *Traquairaspis* is found, and the Primaeva horizon, in which *Pteraspis "primaeva"* (this undescribed species is related to *P. leathensis,* belonging to the same subgenus, *Simopteraspis)* appears, in correlating the horizon with *P. "primaeva"* with the zone with *P. leathensis.* Such close a correlation seems, however, somewhat premature in view of our defective knowledge of the entire vertebrate fauna of both districts.

Of the cephalaspid genera known from the Red Bay series, *Ectinaspis, Tegaspis, Hoelaspis* and *Kiaeraspis* are restricted to Spitsbergen, and cannot, therefore, be used in comparing the Spitsbergen fauna with that of other areas; *Cephalaspis, Securiaspis* and *Benneviaspis* have a wider distribution and accordingly are of importance for the correlation.

The general aspect of the cephalaspid fauna, reflected in the coexistence of the genera *Cephalaspis, Securiaspis* and *Benneviaspis* (with disregard of the above-mentioned special Spitsbergen genera) as well as the general morphological type of the *Cephalaspis* species makes it at once evident that at least the Ben Nevis division can broadly be correlated with the Dittonian of England, as was done by Säve-Söderbergh (1941b, p. 239) and Føyn & Heintz (1943, p. 44) who all, of course, use the terms Downtonian and Dittonian in the sense of King.

In the cephalaspid fauna of the Fraenkel Ridge division the typical Dittonian genera *Benneviaspis* and *Securiaspis* are absent; the *Cephalaspis* species are, in general, of the same type as those from the Ben Nevis division and from the English Dittonian, and, as pointed out first by Säve-Söderbergh (1941b, p. 239; see also Føyn & Heintz 1943, p. 44), the typical Lower Downtonian cephalaspid genera are totally lacking here; therefore the fauna of the Fraenkel Ridge division can at most be possibly Upper Downtonian. The cephalaspid fauna of the Upper Downtonian in England is poor and little known; the typical genus *Didymaspis* is lacking in Spitsbergen.

If therefore the general type of the cephalaspid fauna in the Fraenkel Ridge division somewhat undecidedly points to a Dittonian age of the fauna, we have here fortunately two *Cephalaspis* species, the occurrence of which unambiguously indicates this age. The fact is that these two species, *C. cradleyensis* and *C. powriei,* are common to the faunas of Spitsbergen and Great Britain, having been previously described from the Old Red of England and Scotland, respectively.

Yet we must remember that we know nothing of the vertical range of these species, which, however, in general seems to be rather limited for *Cephalaspis.* On the other side, we must not underestimate the occurrence of identical species in two areas with (for the rest) faunas of rather similar composition; ordinarily, in correlating continental faunas, we have only to do with genera or combinations of genera of supposed contemporaneous occurrence.

C. cradleyensis, known from the Dittonian of England, is found in the lower part of the Fraenkel Ridge division, in the Plant horizon, and *C. powriei,* from the Lower Old Red sandstone of Scotland, occurs, as a distinct variety (var. *polaris)* in the Anglaspis horizon, and thus in the uppermost part of the same division.

C. cradleyensis is recorded from the stratum II.1 in King's table (Stensiö 1932, pp. 200, 203), and, although it is indicated by White

(1950a, p. 52; 1950b, fig. 1, cf. p. 88), that this "*Cephalaspis* sandstone-cornstone" (II.1) is diachronic and may in places occur so far down in the series as to correspond to an upper part of King's I.9, it seems from a passage by King (in Stensiö 1932, p. 200) that the locality (Ridgeway Farm near Cradley in Herefordshire) from which *C. cradleyensis* comes, must lie considerably above the stratum I.9. *C. cradleyensis* is here, at Cradley, found in association with *C. salweyi, C. agassizi, C. sollasi, C. fletti?, C. langi?, Benneviaspis lankesteri* and *B. anglica,* and this fauna (with *Benneviaspis* and *Cephalaspis)* places the locality up in the zone with *Pteraspis crouchi* (see White 1950b, fig. 1).

The second species, *C. powriei,* which is rather polymorphic is found in several localities in Forfarshire and Pertshire in Scotland; these localities cannot be fitted into their proper place in the type-profile (from England) of the Lower Old Red, but they are in any cases not older than the Dittonian (in the sense of King, see Stensiö 1932, pp. 201, 203).

We can furthermore note that several of the *Cephalaspis* species from the Fraenkel Ridge division are closely related to species from the Dittonian in England, viz. *C. pygmaea* which is extremely similar to *C. heightingtonensis* (from II.3) and also resembles *C. langi; C. oreas* similar to *C. whitei* (from II.1—3), and *C. hyperboreus* probably nearly akin to *C. fletti* (II.1—2).

We can thus safely incorporate the major part of the Fraenkel Ridge division (at least as far down as to the Plant horizon, inclusive) with the Dittonian. As furthermore the two *Cephalaspis* species, found in the underlying Corvaspis horizon, are identical with species in the upper part of the division *(C. acuminata,* also in the Primaeva and possibly in the Anglaspis horizons; *C. dissimulata,* also in the Primaeva, the Polaris, and the Anglaspis horizons) there is every reason to consider also this part of the series to be Dittonian. The lowermost fossiliferous horizon, the "Psammosteus" horizon, contains two *Cephalaspis* species *(C. corystis,* the other unnamed, p. 426) which differ in no way markedly from the species in the other parts of the Red Bay series. *C. corystis* is closely connected with *C. hastata, C. ibex* and probably *C. signata* from the upper part of the Fraenkel Ridge division and from the Ben Nevis division, and apparently most closely related to *C. isachseni* from the lowermost part of the Wood Bay series. If we take into account only the Cephalaspids for the determination of the age of this horizon, we can find no reason to refer it to another series than the remaining part of the Red Bay deposits but must include it, too, into the Dittonian.

Against such a correlation some objections may be raised if we take into consideration the other vertebrate fossils from these layers.

So has White (1950b, pp. 85—86) laid stress on the occurrence of *Traquairaspis* and *Corvaspis* in horizons below the Primaeva horizon (with *Pteraspis "primaeva";* see above, p. 579). In England *Traquairaspis* is confined to two zones in the upper part of the Downtonian, and *Corvaspis* to the uppermost zone in the Downtonian. There is, however, no specific identity between the English and the Spitsbergen forms of these two genera (as far as I have seen, after a cursory view of the material from the Spitsbergen deposits in the Palaeontological Museum, Oslo). According to Føyn & Heintz (1943, p. 42) *Corvaspis* is in Spitsbergen known also from the lower horizons of the Ben Nevis division, and the genus thus occurs there in layers that are distinctly younger than that to which it is restricted in England; the stratigraphical importance of the genus is evidently overrated (cf. Stensiö 1944, p. 4). Although the genus *Traquairaspis* is known in Great Britain only from Downtonian deposits, its occurrence in a certain horizon in Spitsbergen cannot a priori be taken as a definite proof of a Downtonian age of this horizon. In this question I base my opinion as to the age of the "Psammosteus" horizon more upon the occurrence of two *Cephalaspis* species, one of them being of a rather specialized type, than upon the presence of the genus *Traquairaspis,* at least until the representatives of this genus in Spitsbergen have been fully described and compared with their congeners in Great Britain, and until the nature of the so-called *Cephalaspis* species from the Downtonian of England (White 1950a, pp. 53, 56) has been made clear.

The genus *Anglaspis* is known in England (see White 1950a, p. 56) from the uppermost zone of the Downtonian up into the zone of *Pteraspis crouchi* (according to White 1950a, fig. 1), and *Poraspis,* earlier known from this zone, descends (also according to White 1950a, fig. 1) into the zone below that of *Traquairaspis symondsi;* these two genera are consequently of little stratigraphical value in this question.

The Wood Bay series. If the age of the Red Bay series can "be determined with a fair degree of certainty, the opposite is the case with regard to the Wood Bay series" (Føyn & Heintz 1943, p. 45).

The rich cephalaspid fauna now known from this series is of very little importance for the correlation with other areas. This is due to the fact that in W. Europe where the Upper Eodevonian and Mesodevonian type profile is developed (see Gross 1933a, p. 56; 1933b, p. 7; 1937 p. 7; 1950, pp. 58—59, 61) Cephalaspids are extremely rare in the marine deposits, younger than the Dittonian. Cephalaspid faunas from other localities are either not adequately or not at all described, or the age of the localities is not definitely settled (e. g. the faunas from W. Podolia and from the Gaspé sandstone in E. Canada). Vertebrate fossils from the Uppermost Eodevonian and from the Lower Mesodevonian are on the whole most uncommon, and this makes the dating of parts of the Old Red deposits in Spitsbergen very difficult.

The question as to the age of the Wood Bay series has been exhaustively discussed by Føyn & Heintz (1943, pp. 45—48). They refer (p. 47) the C. Kjeldsen division to the "Lower Lower Devonian" (= Siegenian) because it forms the lower part of an at least partly Eodevonian series which rests conformably upon beds of Dittonian age. The large Pteraspid *"Gigantaspis"* (not yet described) which occurs in the C. Kjeldsen division is said (Føyn & Heintz 1943, p. 45; see also Heintz 1937, p. 17) to be related to *Pteraspis (Archaeoteuthis) dunensis* and *P. cornubica;* these two species are known from the Upper Eodevonian. Phlyctaenaspids are abundant in the Wood Bay series but are represented by forms known only from Spitsbergen, and cannot be used as basis for a more accurate correlation. From the upper parts of the series are recorded finds of Placoderms, otherwise known as exclusively Mesodevonian forms, as *Homostius, Heterostius* and *Actinolepis* (Føyn & Heintz 1943, pp. 19, 28, 36, 40, 45—47; see also Heintz 1937, pp. 17—18).

With regard to the Cephalaspids we can note that the genera *Boreaspis, Axinaspis, Acrotomaspis* and *Nectaspis* are exclusively Spitsbergen forms; *Cephalaspis* and *Benneviaspis* are found in other areas. A cornu, referred to *Cephalaspis diensti* by Gross (1933a, pl. 3:8) from the Siegenian in the Rhineland is of the same type as that of several species from the Wood Bay series, thus very broad and with the lateral sensory field rather narrow and lying near to the lateral margin of the shield; the fragment is in fact fairly similar to *C. laticornis* or *C. caroli* from the C. Kjeldsen division.

We can furthermore note that *C. moy-thomasi* from the Stjørdalen division of the Wood Bay series is, as far as can be judged, very similar to *C. dawsoni* (Lankester 1870b) from the Gaspé sandstone. The age of this formation is, however, much disputed; earlier generally regarded as Eodevonian, it is considered by Alcock (1935, pp. 8, 79) to be Mesodevonian, and at least partly Lower Mesodevonian, by Kindle (1938, p. 44) in the parts here concerned to be Upper Mesodevonian (contemporary to the Hamilton formation of New York), and by Cooper (1942, p. 1760; cf. pp. 1732, 1764, 1780, table; with criticism of the interpretations of Kindle) as Upper Eodevonian (a sandstone facies of the Onondaga, or equivalent to the Schoharie deposits which are a part of the Onondaga, the latter being regarded as probably corresponding to the Emsian; cf., however, Kayser & Brinkmann 1948, table opposite p. 70).

It can furthermore be noted that *Benneviaspis* species of the type, represented by *B. grandis,* are found in W. Podolia, in layers which are regarded (by Brotzen 1936) as being of Lower Siegenian age.

In principal agreement with the views of Føyn & Heintz (1943) I here regard at least the lowermost part of the C. Kjeldsen division as belonging to the Siegenian. The questions as to the upper limit of this series in Spitsbergen (which may not necessarily coincide with the upper boundary of the lower part of the C. Kjeldsen division) and whether the upper part of the C. Kjeldsen division is of Siegenian or of Emsian age and, then, whether an upper part of the Wood Bay series can be regarded as belonging to the Mesodevonian or not, cannot, for the time being, be answered.

The Grey Hoek series. Also the age of the Grey Hoek series cannot be determined at present. The two Cephalaspids recorded from this series are of no stratigraphical value. The series has generally been classified as Mesodevonian (see above), and it seems natural from its position below the Upper Mesodevonian Wijde Bay series to regard it as being of Lower Mesodevonian age, but a safe palaeontological basis for such an assumption is lacking.

Finally we may also make a few remarks on the Devonian vertebrate fauna of W. Podolia (see Alth 1874; Brotzen 1933a; 1933b; 1934; 1936; Paucă 1941; Stensiö 1934; 1942; 1944; 1945; Zych 1927; 1931; 1937) in comparison with that of Spitsbergen.

The cephalaspid fauna of W. Podolia is rich but as yet only two species have been described (Zych 1937; Paucă 1941, p. 29). Stensiö (1945, p. 3) mentions *C. woodwardi* and a species akin to *C. salweyi.* I have seen some of the Cephalaspids collected there which partly have been preliminarily worked up by Zych. In this material, besides the forms just mentioned, a species (from stage I; see below) very near to, if not identical with *C. jacki* (from the zone with *Pteraspis crouchi* in England), a species (from stage I) near *C. hoeli,* one additional species (from stage I) similar to *C. salveyi,* and a species very near to *C. ibex,* can be mentioned, as well as representatives of *Benneviaspis* (a species from stage I very similar to *B. longicornis,* cf. p. 449, and two species, at least one of them from stage III, of the same type as *B. grandis* and *B. lövgreeni)* and *Securiaspis* (a large form from stage I).

These Westpodolian layers (cf. Zych 1927; Kozlowski 1929, pp. 1—25; Văscăutanu 1931; Brotzen 1933b, pp. 425—428; 1936, pp. 2—7; Arabu 1941; Samsonowicz 1951, pp. 499—504; etc.), which form the upper western parts of a long series of deposits all the way from the Ordovician in E. Podolia, show the transition from the Silurian to the Eodevonian, and, as is generally assumed, at the same time from marine to continental facies. The marine deposits of W. Podolia have been divided into several stages by Kozlowski (1929, pp. 1—25) on the basis of the vertical distribution of the Brachiopods. The uppermost stage, the Czortków stage, is provisionally considered as a whole to correspond to the Downtonian. The vertebrate fauna of this stage (see

e. g. Brotzen 1936, p. 6; Stensiö 1944, pp. 3—4), however, strongly suggests a Dittonian age of the strata (cf. Gross 1950, pp 48—49); it can also be mentioned in this connection that already in the underlying Borszczów stage there appear representatives for several Brachiopod genera, generally considered to be exclusively Devonian (Kozlowski 1929, pp. 16—17). The following continental deposits are divided into three stages (I—III) by Brotzen (1936, pp. 3—7) mainly on the basis of the vertical distribution of the Pteraspids; the stages I—II are referred to the Gedinnian by Brotzen, and the stage III (which is especially characterized by the presence of two species of the (sub)genus *Archaeoteuthis)* to the Lower Siegenian.

A closer comparison of the Spitsbergen vertebrate faunas with those of W. Podolia is precluded since they are too imperfectly or unequally known. The Red Bay series seems to correspond broadly to the Czortków stage and stage I. The lower part of the C. Kjeldsen division has its approximate equivalent in the stage III (it is here of special interest to note the occurrence in both these layers of *Benneviaspis* species of the same type, with strongly developed sensory fields).

In conclusion we may say that the various cephalaspid species in Spitsbergen seem to have a rather restricted vertical distribution and to characterize many of the layers in the Old Red deposits here.

Their occurrence cannot, however, alone form the basis for a stratigraphical subdivision of these strata but this can be done safely first after the working up of the other vertebrate fossils found. The whole vertebrate fauna must furthermore be taken into consideration for a safe correlation with other areas. The Spitsbergen Cephalaspids are in general of fairly little importance in this respect as the species apparently were not very widespread (only two foreign species, described from Great Britain, are refound in Spitsbergen) and as they in other areas with supposed contemporary deposits, except in Great Britain, are rare or not adequately studied. A further difficulty in the correlation is that we have as yet no type profile through continental deposits of Upper Eodevonian and Lower Mesodevonian age, based on the vertebrate faunas of these times.

The cephalaspid fauna of the Red Bay series, however, suggests that the whole sequence of fossiliferous strata in this series (the lowermost one of the Spitsbergen Old Red) belongs to the Dittonian and that thus the Old Red in Spitsbergen is possibly altogether of Devonian age.

Summary.

A rich material of Cephalaspids from the Spitsbergen Old Red is treated in this paper, to a large extent from a systematic point of view (pp. 237—549). Numerous observations upon the external and internal morphology are recorded (pp. 26—235) but no attempt is made to give a comprehensive description of the organization of the Osteostraci.

The main points in the paper can be summarized as follows (nos. 1—18).

1. The general form of the cephalic shield is described and is found to be rather variable. Some forms lacking cornua occur (pp. 26, 33). The face of the pectoral area is described (pp. 34—37) in two different forms, one of them with cornua and well developed pectoral sinus, the other without pectoral sinus and the cornua replaced by lateral angles on the shield; both forms had possessed pectoral fins (cf. no. 8). The number of the lateral sensory fields (no. 11) is variable within the family, and there are found one, two, three or four pairs of such fields. In certain cases some variations exist in this respect even within the species (pp. 28, 509, 520). In some forms the middle division of the naso-hypophyseal opening is obliterated, and there are separate openings for the nasal and the hypophyseal ducts (p. 29). Some species had an independent pineal plate; in others (and mainly in later forms) such a plate was absent (p. 31).

2. The minute structure of the exoskeleton is reviewed in different forms (pp. 40—52). In numerous species the mucous canal system consists of a fine-meshed network while the horizontal vascular canals in the lower division of the middle layer are disposed as radiating canals. In some genera *(Benneviaspis, Hoelaspis, Boreaspis)* the vascular canals too are disposed as a fine-meshed network. No general correlation exists between the disposition of the mucous and the vascular canals. The grooves of the sensory lines, which in the Spitsbergen Cephalaspids reach down into the outer division of the middle layer, are in communication with the grooves or canals of the mucous canal system but this relation is only topographical, and from a structural point of view the two systems were certainly quite different (pp. 48—50). The exo-

skeletal plates of the sensory fields consist of free plates which in general are not attached to each other or to the rest of the shield; in their minute structure they differ from the exoskeleton of the rest of the shield only in having wide cavities in the basal layer (p. 48). No general tendency towards a reduction of the exoskeleton can be observed in the geologic history of the Osteostraci.

3. In the continuous endoskeleton, in which previously (Stensiö 1927) the endocranium, the dorsal part of the visceral endoskeleton, the zonal endoskeleton or the endoskeletal shoulder-girdle and the pronephros component have been recognized, the following additional divisions are distinguished, viz. the dorsal and lateral inter-zonal endoskeleton and the inter-zonal axial endoskeleton (pp. 54—57). The lateral inter-zonal endoskeleton, which is an ossification in the lateral fin-fold and of the same nature as the zonal endoskeleton, is not distinguished in the Spitsbergen Cephalaspids (but is present in the Silurian *Dartmuthia)*. The dorsal inter-zonal endoskeleton forms an ossification in the dorsal fin-fold, and is present i. a. in the dorsal spine. The inter-zonal axial endoskeleton passes anteriorly over into the occipital region of the endocranium (as does also the dorsal inter-zonal endoskeleton), and the boundary-line between these two divisions is arbitrarily drawn between the vagus canal and the canals for the first spinal nerve (p. 56).

4. The canals and cavities in the different regions of the endocranium are considered (pp. 57—103). Several new interpretations, at variance with those of Stensiö (1927), are put forward; some of them are of great importance for a new conception of the morphology of the (anterior part of the) head in the Osteostraci (cf. nos. 6, 12): the part of the cranial cavity assumed to have lodged the telencephalon is thought to have contained the olfactory organ (p. 58); "the canal for the n. profundus" is considered to be the canal for the r. maxillaris trigemini (pp. 62—63); some superficial canals are interpreted tentatively as canals for the n. profundus (p. 60); "the canal for the n.trigeminus proper" is the canal for the r.mandibularis trigemini (pp. 64—66); the fossa interpreted as a myodome is regarded as a compartment which lodged the ganglia for the n. profundus, the n. trigeminus proper and the n. lateralis anterior, it is called the trigeminus-lateralis chamber. (p. 68). A re-interpretation of the canals in *Cephalaspis,* entering this chamber from the brain cavity is given (pp. 68—78): "the canal for the somatic sensory root of the n. trigeminus proper" is interpreted as the canal for the anterior lateralis root, "the canal for the somatic sensory root of the n. profundus" as the canal for an anterior cerebral vein, "the canal for the visceral motor root of the n. profundus" as the canal for the sensory trigeminus (s. l.) root (in some cases a small canal for the profundus root is present), and "the canal for the v. pituitaria"

as the canal for a branch of the anterior cerebral vein. “The canal for the r. saccularis n. acustici” is considered to be the canal for the v. labyrinthi posterior (p. 81). A widening of the basalmost part of the canal for the first nerve to the lateral sensory field at the transition to the vestibulum and some depressions in the floor of this cavity are interpreted as having been caused by the ganglia of the nerves to the lateral sensory field (pp. 84—85; cf. nos. 11, 12). The so-called vestibulum was filled to a large extent with these ganglionic masses and was not occupied by the membranous labyrinth organ. Canals for an unpaired a. spinae dorsalis (a. cristae dorsalis) with paired origin from the aorta on a level with the occipital region are described (pp. 88—89). The canals connected or associated with the vagus canal are described in detail in a *Cephalaspis* species (pp. 89—97). In this species the main canal for the n. glossopharyngeus runs behind and laterally to the vestibulum. Some canals are considered to be canals for lateralis (and general cutaneous) branches associated with the n. glossopharyngeus and canals for the r. lateralis vagi. An offshoot from the aortal canal for an artery, here called the a. segmentalis occipitalis, divides into a branch, which gives rise to the canals for the (two) posterior dorso-lateral superficial arteries, and a branch, which closely follows the canal for the main n. glossopharyngeus and opens into the groove for the third efferent branchial artery in the roof of the oralo-branchial chamber. This branch, called the canal for the a. communicans, sends off i. a. the canals for the anterior dorso-lateral superficial arteries, and some small canals for the aa. vestibulares. Also in *Nectaspis* the canal for the n. glossopharyngeus (and the a. communicans) runs outside of the vestibulum, but in general the canal for the n. glossopharyngeus and the a. segmentalis occipitalis opens into the posterior part of the vestibulum, and a canal for the distal part of the n. glossopharyngeus and the a. communicans as well as canals for the anterior and posterior dorso-lateral superficial arteries issue from the lateral part of the vestibulum; the large distal “canal for the n. glossopharyngeus” (Stensiö 1927) had thus also lodged the a. communicans.

5. With regard to the dorsal superficial parts of the visceral endoskeleton the disposition of the artery canals (lateral branches of the a. adorbitalis, by Stensiö regarded as the main stem of the a. facialis, and anterior and posterior dorso-lateral superficial arteries), the vein canals and the nerve canals are reviewed (pp. 117—129). The canals for the lateral sensory field (or fields) are five in number (the first one often divided into two main branches); they are of a rather uniform disposition in all the different forms of the family (pp. 128—129).

6. The conditions in the anterior part of the roof of the oralo-branchial chamber are described in detail in a *Cephalaspis* species

(C. signata; pp. 129—148). In this species the gill-apparatus has left various impressions in the roof. There are i. a. impressions of the gill-apparatus proper, of the external efferent ducts, and of structures supposed to have been the gl. thymus. A groove in the first branchial fossa is interpreted as (probably) that for the peripharyngeal ciliated groove. Grooves for efferent and most probably also for afferent branchial arteries are preserved as well as small grooves for arterioles. A small groove in the first branchial fossa is called the groove for the a.spiracularis (= the real first efferent artery). The aorta was continued forwards by the (at first) unpaired a. rostralis, and grooves in front of the first branchial fossa are interpreted as grooves for branches of this artery, and other grooves as those for the paired a. rostralis. In other species these latter grooves run in lateral direction to the canal for the a. marginalis (pp. 148, 154). Grooves for a bucco-pharyngeal vein and for vv. nutritiae branchiales are described. Several grooves for the r. maxillaris V, r. mandibularis V, n. facialis, n. glossopharyngeus and for some of the branchial rami of the n. vagus are described (pp. 144—148, 150—152). The posterior portion of the oralo-branchial chamber is described in another *Cephalaspis* species *(C. exilis,* pp. 148—150). In *Cephalaspis* (and others) an unpaired canal for the a.efferens communis (impar) is found (as described by Stensiö 1927) but in *Boreaspis* the canals for the paired a. efferens communis open directly into the aortal canal (p. 163). In *Cephalaspis* the three anterior efferent arteries joined the aorta dorsalis directly; the canals for the fourth and following efferent arteries open into the canal for the paired a. efferens communis (pp. 149—152). The canals interpreted by Stensiö as those for the fourth—sixth efferent arteries are here considered to be the canals for dorsal nutrient branchial arteries (p. 153). In *Nectaspis,* in which the anterior portion of the oralo-branchial chamber is described (pp. 154—158), a strong ridge, here called the velar ridge (in part corresponding to the velum in recent Cyclostomes) partly divides the oralo-branchial chamber into a buccal cavity and a branchial chamber proper. The velar ridge was pierced by the r. maxillaris V. In *Cephalaspis* and other genera the velar ridge is slightly developed, and the buccal area in front of it is almost smooth (when not provided with grooves for the marginal and rostral veins). Nine branchial fossae are generally developed. In *Boreaspis* no real velar ridge is developed, and the buccal area and the first branchial fossa form a large continuous surface. The oralo-branchial chamber and especially its lateral parts with the branchial cavities are described in this genus (pp. 158—163); here traces of only seven branchial fossae have been found. It must be observed that a cavity, corresponding to the presumed "first branchial fossa" in *Kiaeraspis,* by Stensiö (1927) said to have lodged a prespiracular gill-sac, is entirely absent in *Cephalaspis* and *Boreaspis* (and

most probably in other genera). In *Nectaspis* the lateral part of the buccal cavity has a distinct fossa buccalis, here considered possibly to have been the fossa for some buccal muscles (p. 156). A most important conclusion from the observed facts in the anterior part of the visceral endoskeleton is that the Cephalaspids had no prespiracular gill-sac; the first one present had a spiracular position (and corresponded to the first visceral pouch in *Petromyzon)*. This is also consistent with the interpretation here put forward with regard to the canals for the n. trigeminus (no. 4; cf. no. 12). The Cephalaspids do not occupy an exceptional position within the vertebrates with regard to the development of the anterior visceral parts of the head, but are in this respect in close agreement with the recent Cyclostomes (pp. 169—170).

7. In the inter-zonal endoskeleton many small canals issuing from the neural canal are described (pp. 104—109). Some of them are considered to be canals for anterior transformed vertebro-medullar veins; such are the canals interpreted by Stensiö as "canals for the dorsal root of occipito-spinal nerves". "The canal for the ventral root of the second occipito-spinal nerve" (Stensiö) is the canal for the dorsal root of the first spinal nerve. In a *Cephalaspis* species a series of canals in the inter-zonal part are described and considered to be those for dorsal segmental veins, entering the dorsal spine (p. 110). In *C. doryphorus* there are canals for two arteries to the dorsal spine; one of them issued (together with the a. segmentalis occipitalis) from the cranial division, the other from the trunk division of the aorta (p. 112). Two pairs of superficial canals are described (pp. 113—115) as the canals for the vv. inter-zonales lateralis and medialis. In the ventral face of the inter-zonal endoskeleton are some grooves for the lateralis nerves to the main lateral line (and the extra-lateral line) and to the dorsal lateral line (pp. 115—116).

8. In the zonal endoskeleton the canals of its median part in *Cephalaspis kozlowskii* (which previously were described by Zych 1937) are reviewed and re-interpreted (pp. 171—173). The corresponding canals and the canals for arteries and veins of the lateral zonal endoskeleton (= the cornu) are described in detail in *C. vogti* (pp. 173—176). The dorsal superficial arteries (here called the aa. scapulares) most probably arose from a segmental artery (of which a groove and a canal are found in *C. excellens;* p. 99); the dorsal superficial vein (here called the v. scapularis) arose from the post-zonal part of the marginal vein sinus. The vein canals of the cornu originate, that for the v. cornualis medialis from the canal for the v. brachialis, and that for the v. cornualis lateralis from the canal for the v. marginalis. The canals piercing the posterior wall of the pectoral sinus (transmitting vessels and nerves for the pectoral fin) are described in *C. ibex* (pp. 178—179) and in *Axinaspis* (pp. 180—181). In the latter genus

there are two independent canals for brachial arteries issuing from the canal for the a. subclavia. As the canals for brachial vessels are well developed in *Axinaspis* and in *Nectaspis* (which both lack real cornua and pectoral sinus) pectoral fins must have been present in them.

9. Indistinct traces of the pronephros component are described in *Axinaspis* (p. 184).

10. The grooves of the sensory line system are described (pp. 184—192), and an attempt towards a homologization with those of *Petromyzon* and of the Heterostraci is made (pp. 191—192). Some lines, not known previously, are observed: a line near the openings for the nasal and the hypophyseal ducts, considered to be a supraorbital line, is found in *Cephalaspis excellens* (p. 189); a dorsal lateral line is described in *C. doryphorus* (p. 189), and in several *Cephalaspis* species a line which is thought to be the anterior portion of the extra-lateral line is found (p. 188); the extra-lateral line is also observed in *Thyestes verrucosus* (pp. 188, 552).

11. The fields interpreted by Stensiö (1927) as "electric fields" are sensory fields of unknown function. Comparisons with conditions in recent fishes lead to a suggestion that they were a specialized part of the lateralis system (pp. 192—198).

12. A resumé of what is known of the cranial nerves in the Osteostraci and a restoration of these nerves are given (pp. 198—210; fig 20). The nerves were developed in the main as in recent Cyclostomes. It is most important to note that the composition of the n. profundus and of the n. trigeminus proper must have been essentially as in this group (and as in other lower vertebrates). The n. profundus was thus not a branchial nerve but contained only somatic sensory fibres. The n. trigeminus was divided into a mixed r. maxillaris and an exclusively motor r. mandibularis. The n. facialis, n. glossopharyngeus and n. vagus were typical branchial nerves. There existed an anterior and a posterior n. lateralis; the ganglion of the former lay closely associated with those of the n. trigeminus. The nerves for the sensory fields were ganglionic in their proximal part, and most of the ganglia was situated within the labyrinth cavity.

13. The disposition of the arteries and the veins in the cephalic shield is reviewed after the interpretations of the canals for these vessels (pp. 210—230). The results are summarized in the restorations of the main arteries and veins given in figs. 21A, B. Some comparisons with vessels in the Cyclostomes and other lower vertebrate groups are made or discussed.

14. The scale-covered trunk division is described in *Cephalaspis pinnifera* (pp. 231—235). This species is provided with a high fin-like dorsal crest, composed of unpaired scutes.

15. As for the systematic part, all the Spitsbergen Cephalaspids are considered to belong to one family: Cephalaspididae, and to the subfamily Cephalaspidinae. A revised diagnosis of the family is given (p. 237), and the characters and the range of the family is discussed (mainly with regard to the concept by Stensiö 1932). The subfamilies "Cephalaspinae" and "Kiaeraspinae" of Stensiö are untenable. The family can be divided into the subfamilies Ateleaspidinae and Cephalaspidinae (cf. Heintz 1939) but no further subdivisions are feasible. The subfamily Cephalaspidinae contains the genera *Cephalaspis, Securiaspis, Benneviaspis, Hoelaspis, Boreaspis, Kiaeraspis, Tegaspis, Ectinaspis, Axinaspis, Acrotomaspis,* and *Nectaspis,* which all are found in Spitsbergen. The last five of the named genera are described as new in this paper. *Benneviaspis, Hoelaspis* and *Boreaspis* are considered to be closely related; possibly *Ectinaspis* is akin to them. *Tegaspis* and *Securiaspis* are probably closely related to *Cephalaspis. Kiaeraspis, Axinaspis* and *Acrotomaspis* are considered to be allied to each other. *Nectaspis* seems to stand comparatively isolated.

In *Cephalaspis* (p. 243) 50 species are found in the present material (36 from the Red Bay series and 14 from the Wood Bay series), 39 are described as new species, and one variety is erected. Two of the *Cephalaspis* species *(C. cradleyensis* and *C. powriei)* were previously known from Great Britain. The genus *Securiaspis* (p. 427) contains two named species (one new species). *Tegaspis* (p. 437) is erected for a species *(T. kolleri* Stensiö) previously included in *Cephalaspis. Ectinaspis* (p. 442) is founded on a single new species *(E. heintzi). Benneviaspis* (p. 446) includes three named species from the Red Bay series and three from the Wood Bay series (five species are described as new). *Hoelaspis* (p. 467) and *Kiaeraspis* (p. 517) contain each the type species only, of which new restorations are given. In *Boreaspis* (p. 472) 13 species are recognized (12 are new species). *Axinaspis* (p. 521) is founded on a single, new species *(A. whitei). Acrotomaspis* (p. 529) contains two named species and *Nectaspis* (p. 537) three species (all new species).

16. The systematic position of the other genera in the Osteostraci is discussed (pp. 550—558), and an attempt is made to assign them to different families. The position of the family Cephalaspididae is indicated in a preliminary table of the families of the group (p. 559).

17. The relations of the Osteostraci to other groups in the subphylum Agnatha is considered (pp. 559—567), and they are found to constitute a separate group, placed side by side with the Anaspida and the Cyclostomata as agnathous monorhinous vertebrates in contrast to the agnathous diplorhinous Heterostraci.

18. In a chapter on the stratigraphy (p. 568) two tables (pp. 570, 571) are given in order to show the vertical distribution of the Cephal-

aspids in the different divisions and horizons of the Spitsbergen Old Red. Comparisons with other areas, especially with Great Britain, are made (pp. 576—585). On the basis of the distribution of the Cephalaspids the whole fossiliferous sequence of the Red Bay series can be referred to the Dittonian (p. 581), and it is suggested that the Old Red of Spitsbergen is entirely of Devonian age. At least the lowermost part of the Wood Bay series (= the lower part of the C. Kjeldsen division) is of Siegenian age (p. 584). The age of the rest of the Wood Bay series and of the Grey Hoek series cannot be settled with the aid of the Cephalaspids.

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Addendum.

The Cephalaspids, collected by the English-Norwegian Swedish Expedition to Spitsbergen in 1939, and in the present paper referred to under the notations ENS nos. 1—616, have now (after the paper had been set up) been divided between the British Museum (N.H.), London, the Palaeontological Museum, Oslo, and the Swedish Museum of Natural History, Stockholm.

The assignment of the material to these institutions is as follows:

The British Museum (Natural History), Department of Geology, London:

ENS nos. 12—14, 17, 19—20, 31—32, 39—40, 42—43, 60—80, 104—105, 114—116, 118, 133—140, 149—155, 167, 170, 174, 177—178, 181, 184, 190—191, 218—219, 221—235, 244—248, 251, 254, 257—260, 264, 267, 274, 276, 281, 305—306, 322—326, 335—336, 352—354, 363—364, 372—382, 394—401, 407—410, 430—431, 434—435, 440—441, 444—445, 451, 454, 457—459, 462, 466—467, 469, 475, 477, 481, 486, 493, 495, 503, 506, 512—514, 517—520, 526, 529—530, 533, 538—539, 544—545, 549, 551, 553—554, 572—573, 584—587, 589—591, 595—596, 600—606, 610.

The Palaeontological Museum, Oslo:

ENS nos. 8—11, 15—16, 21, 28—30, 33—35, 41, 82—103, 112—113, 117, 119—132, 158—161, 165, 168, 172, 175—176, 183, 185, 188, 193—194, 208—217, 220, 237—239, 252—253, 255—256, 265—266, 269, 271—273, 277, 280, 283, 300—302, 307, 309—319, 321, 327—330, 337—338, 349—351, 357—358, 365—371, 389—391, 404—406, 423—429, 436, 439, 442—443, 448, 452, 455—456, 460, 463, 465, 470—472, 479, 484, 488—491, 494, 496—502, 507—510, 521—523, 532, 535, 541—542, 548, 550, 552, 555—556, 558—565, 567—571, 574, 577—581, 588, 592, 594, 608, 611.

The Swedish Museum of Natural History, Department of Palaeozoology, Stockholm:

ENS nos. 1—7, 18, 22—27, 36—38, 44—59, 81, 106—111, 141—148, 156—157, 162—164, 166, 169, 171, 173, 179—180, 182, 186—187, 189, 192, 195—207, 236, 240—243, 249—250, 261—263, 268, 270, 275, 278—279, 282, 284, 303—304, 308, 320, 331—334, 339—348, 355—356, 359—362, 383—388, 392—393, 402—403, 411—422, 432—433, 437—438, 446—447, 449—450, 453, 461, 464, 468, 473—474, 476, 478, 480, 482—483, 485, 487, 492, 504—505, 511, 515—516, 524—525, 527—528, 531, 534, 536—537, 540, 543, 546—547, 557, 566, 575—576, 582—583, 593, 597—599, 607, 609, 612—616.

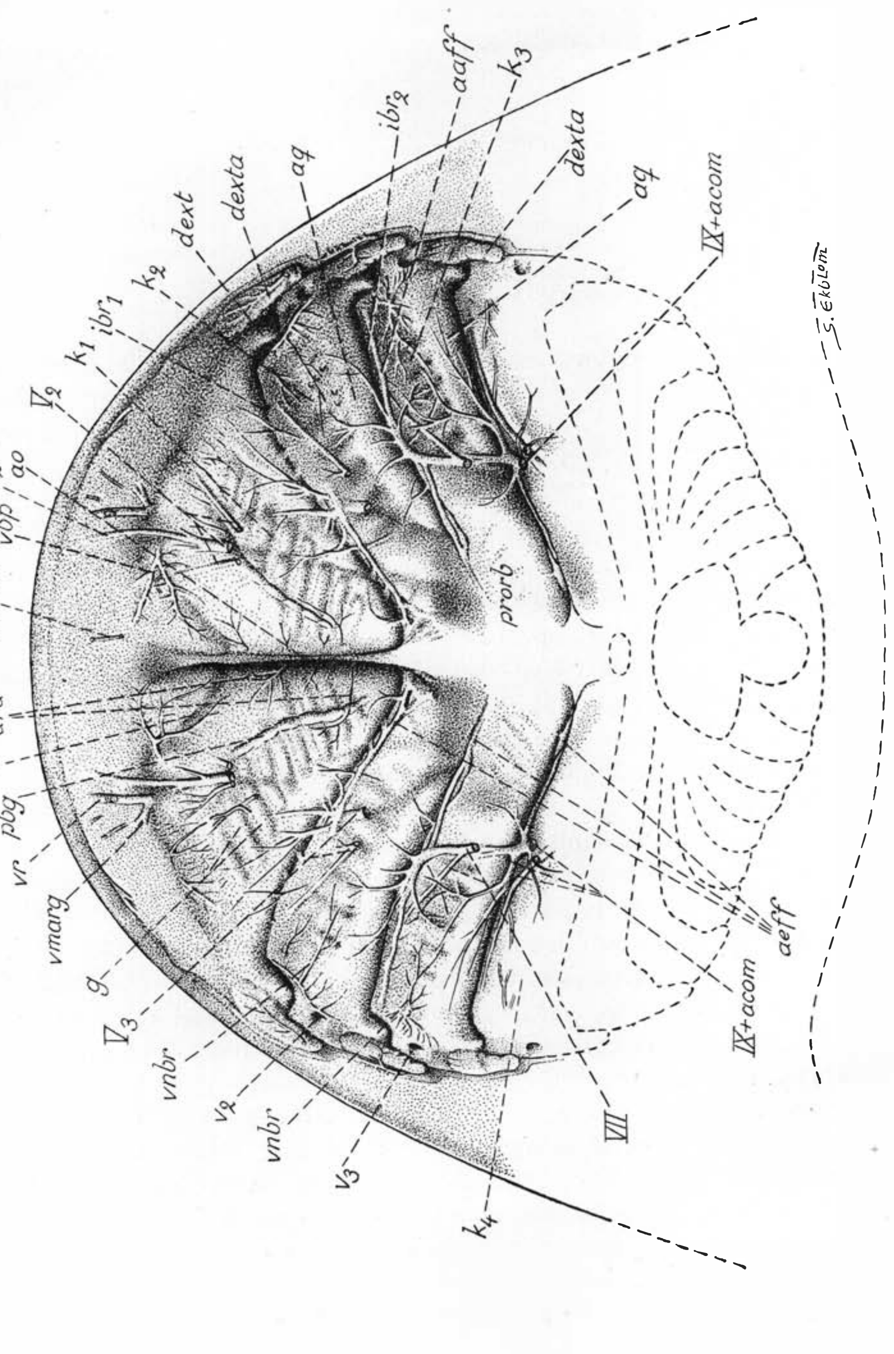
Supplementary note.

During the long time that has passed since this paper was sent to the press I have had the opportunity to become acquainted with certain special researches on fossil lower Gnathostomes now going on in the Palaeozoological Department of the Swedish Museum of Natural History in Stockholm. These researches have necessitated a re-examination of the Cephalaspids with regards to the visceral endoskeleton and its nerves. As a result hereof it has appeared that the conditions in the oralo-branchial chamber of *Cephalaspis signata* (fig. 14; pls. 27:2; 29:2; 30:1; 32:2; pp. 129—148) have to be interpreted in a way different from what has been done above in the anatomical part of the present paper (cf. pp. 168—170, 589—590). The conclusive interpretations which I have now arrived at (see fig. A) are in accord with those previously put forward by Stensiö (1927; 1932).

Thus the following is now evident concerning the nerve-supply of the oralo-branchial chamber in *C. signata.* The facial nerve *(VII,* fig. A; cf. fig. 14; pls. 27:2; 29:2) innervated the soft parts related to the second interbranchial ridge (ibr_2, fig. A), that is to say its anterior and posterior hemibranchs and their muscles, etc. The glossopharyngeus nerve *(IX)* supplied the corresponding structures of the third interbranchial ridge (ibr_3) and the branchial rami of the vagus nerve the corresponding structures of the remaining posterior interbranchial ridges.

Because of its relations to the facial nerve the second interbranchial ridge (ibr_2) corresponds to the hyoid arch, which means that the first interbranchial ridge (ibr_1) and the prebranchial ridge (*rpm;* = "velar ridge", p. 129) represent the mandibular and premandibular arches, respectively. The branchial fossa (k_2) situated between the hyoid arch and the mandibular arch is therefore a spiracular gill fossa, whereas the branchial fossa (k_1) between the mandibular and premandibular arches is a prespiracular gill fossa.

In view of what has just been set forth it is evident that the nerve (V_3) related to the first interbranchial ridge was the visceral trunk


k1
ibr1
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k3
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vmarg
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vnbr
v3
k4
VII
IX+acom
aeff

Fig. A. — *Cephalaspis signata* n. sp. Cast of the anterior part of the oralo-branchial chamber (the impressions *dexta* partly after a specimen of *C. ibex).* Dorsal view. About × 1½.

aaff, groove probably for a nerve and also for an afferent branchial artery; *aeff,* grooves for efferent branchial arteries; *ao,* impression of aortal ridge; *aq,* thick grooves marking the position of the spaces through which the water was let out from the gills; *ard,* grooves for nutritive arterial branches; *arostr,* groove caused by a vessel, coming from the interior of the endoskeleton; *dext,* recurrent portions of branchial fossae; *dexta,* impressions of glandular organs (possibly the thymus) in the grooves for the external branchial ducts; *g,* impressions of gills; ibr_1-ibr_2, interbranchial ridges 1 and 2, representing the mandibular and hyoid arches, respectively; k_1-k_4, branchial fossae 1—4; *pbg,* groove of uncertain importance (cf. Stensiö 1927, fig. 36; pls. 51, 52); *prorb,* impression of orbital prominence; *rpm,* prebranchial ridge, representing the premandibular arch; *vbp,* grooves probably for veins; *vmarg,* groove for marginal vein; *vnbr,* grooves probably for veins; *vr,* groove for rostral vein; v_2-v_3, openings for transversal veins; V_2, grooves and canals for the visceral trunk of the trigeminus I; this trunk partly corresponds to the nerve currently termed the r.maxillaris; the other trunk of the trigeminus I was the profundus nerve; V_3, grooves for the r.mandibularis V (the visceral trunk of trigeminus II); *VII,* grooves for the n.facialis; *IX+acom,* grooves for the n. glossopharyngeus and for the a. communicans.

of the trigeminus proper or trigeminus II, that is to say the ramus mandibularis V. Hence it follows that the nerve described above (pp. 62—63) as the r. maxillaris V (V_2) and which is related to the prebranchial ridge in fact is the visceral trunk of trigeminus I. As demonstrated above (p. 63) the visceral ramus of the trigeminus I, which at least partly corresponded to the r. maxillaris V of the Cyclostomes and fishes, passed ventrally to the optic nerve. Besides this strong visceral ramus, the trigeminus I in the Cephalaspids also had a dorsal branch, the profundus nerve (V_1, p. 60), which corresponded to the similarly termed nerve of the Cyclostomes and fishes and, like in these, ran dorsally to the optic nerve.

My interpretations of the conditions of the oralo-branchial chamber are elucidated further in detail by fig. A.

The reinterpretations in *Cephalaspis signata* necessitate corresponding reinterpretations in the other Cephalaspids treated in the present work. All these Cephalaspids agree fundamentally with *C. signata* where the interbranchial ridges, the prebranchial ridge, the branchial fossae and the visceral rami of the nerves are considered *(Cephalaspis exilis,* p. 148, pl. 27:1; other *Cephalaspis* species, pp. 164—165, fig. 15B, pls. 26:2; 38:1, etc.; *Nectaspis,* pp. 154—157, fig. 15C, pls. 106—109, 111; *Boreaspis,* pp. 158—160, fig. 15A, pls. 78:2-3, 85, etc.; *Hoelaspis,* p. 165; *Benneviaspis,* p. 166, pl. 71:1; *Axinaspis,* p. 166, pl. 100:1; *Kiaeraspis,* p. 167; *Acrotomaspis,* p. 168, pl. 102:1; *Didymaspis,* p. 168). In these circumstances it is clear that the cavities in *Nectaspis* *(bc, fb,* fig. 15C; pp. 155—156) that I have described as the "buccal cavity" and the "fossa buccalis" in fact are a prespiracular gill fossa.

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