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FAMILY *CEPHALASPIDAE*

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A. W. BRØGGERS BOKTRYKKERI A/S

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BY

ERIK A:SON STENSIÖ

WITH 1 MAP, 103 TEXT-FIGURES, AND 112 PLATES

A. TEXT

CONTENTS

Introduction.

Remains of Devonian fishes were first encountered in Spitsbergen by MALMGREN and A. E. NORDENSKIÖLD at Liefde Bay in 1868. In 1870 NATHORST and WILANDER found fragments of Devonian fishes on the westcoast of Klaas Billen Bay, and in 1882 NATHORST discovered that Devonian fishes were abundant both in the strata at the inner parts of Dickson Bay and in certain strata in Mimer Valley, and brought together rich collections from both these localities. During the Swedish Arctic Expeditions of 1898 remains of a *Pteraspis* (WOODWARD 1900, p. 3) were collected at Grey Hoek and finally in 1899 TSCHERNYCHEW and DE GEER recorded the occurrence of Devonian fish-remains at Horn Sound (cf. NATHORST 1910, p. 315).

The collections of Devonian fishes brought together from Spitsbergen by the Swedish Expeditions up to 1882 were briefly treated by LANKESTER in 1884, but is was not until 1891 that a more detailed description of them was published by WOODWARD (1891 b). The forms distinguished at that time by the latter writer were as follows: *Pteraspis nathorsti* LANKESTER, *Psamosteus arenatus* AGASSIZ, *Acanthaspis decipiens* A. S. WOODWARD, *Acanthaspis minor* A. S. WOODWARD, *Lophostracon spitsbergense* (LANKESTER), *Asterolepis scabra* (A. S. WOODWARD),[1] *Porolepis posnaniensis* (KADE) and *Onychodus arcticus*, A. S. WOODWARD.

In addition to these there were also mentioned several undeterminable remains of Crossopterygians and a fragment of a *Cephalaspis*. This *Cephalaspis*-fragment was from Dickson Bay and had been found by NATHORST in 1882.

No further contributions to the knowledge of the Old Red fish fauna of Spitsbergen were obtained until in 1906, when the Norwegian explorations of North Spitsbergen began. In that year a new fish locality was found by A. STAXRUD in Mt. Pteraspis between Red Bay and Liefde Bay (HOEL 1909, p. 7; NATHORST, 1910, p. 309). In the following year a second fish locality was discovered by HOEL in the

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[1] Named *Asteroplax scabra* by WOODWARD in 1891, but according to the new material collected by me in 1916 and 1917 we are undoubtedly concerned here with a big Antiarch, most probably an *Asterolepis* (cf. STENSIÖ 1918 a, p. 69).

Old Red Sandstone at the inner end of Wood Bay (Hoel 1909, p. 8; Nathorst 1910, p. 309), and this latter locality is the one referred to in the present work as west side of Wood Bay, N. of Hoffnung Glacier. During the subsequent Norwegian expeditions in the summers 1909—1912 a number of other new fish localities were found in northern Spitsbergen, e. g. at Red Bay, at the Reindeer Peninsula, at different places around Wood Bay, at Bock Bay, at Grey Hoek and along the west coast of Wijde Bay. The enormous collections brought together from all these localities consist of remains of Pteraspids, Cephalaspids, Arthrodires (particularly *Acanthaspis*-forms), Elasmobranchs and Crossopterygians (Kiær in the paper by Hoel in 1909, pp. 7, 8, and in 1914; and in Nathorst 1910 p. 309; Kiær 1916).

The Norwegian Spitsbergen expeditions in 1917—1920 devoted much attention to the Devonian deposits between Horn Sound and South Cape and brought together a fairly considerable collection of fish-remains from the southern part of Spitsbergen. These fish-remains appear to consist only of Arthrodires *Acanthaspis*-species, *Coccosteus*-species or other Coccosteids and Crossopterygians (*Porolepis*-like scales).

During the Norwegian expedition of 1924, a collection of Devonian fishes from Mt. Lyktan and from the region between Dickson Bay and Wijde Bay (West Fjord) was brought together.

Finally, in 1925 a Norwegian expedition visited certain of the Old Red fish localities on the north-coast of Spitsbergen as well as the old localities at the Icefjord. The material brought home by this expedition was in many respects very valuable (Vogt 1926). Details of the Norwegian expeditions, 1906—1925, will be found in the tables on pp. VIII—IX.

On the basis of the observations made by Holtedahl and himself in the field, and the preliminary determinations of the fossils which had been made by professor J. Kiær of Oslo, Hoel was in 1912 (Hoel 1913, p. 106) able to subdivide the Old Red deposits in northern Spitsbergen into four series, which have since been termed the Wijde Bay series, the Grey Hoek series, the Wood Bay series and the Red Bay series respectively. Of these the Wijde Bay series was the youngest, the Red Bay series the oldest. Further contributions to our knowledge of the stratigraphy of the Old Red deposits of northern Spitsbergen have since been published by Hoel in 1914 (pp. 15—16), by Holtedahl in 1913 (pp. 707—712), 1914 (pp. 415—424), and 1926 (pp. 23—28), by Kiær in 1916, and Quenstedt in 1926, but it has not yet been possible to make a more detailed subdivision of these deposits than that proposed by Hoel in 1912. According to what is so far known concerning the age of the four series of which the Old Red deposits of Northern Spitsbergen is made up, the Wijde Bay series would be at least partly equivalent to the younger Devonian of the Mimer Valley, while of the other series the Grey Hoek series would be middle Devonian[1], the Wood Bay series lower Devonian, and the Red Bay series Downtonian.

From my observations on the fish-remains from Horn sound it seems most probably that the Devonian deposits in the vicinity of that fiord are yonger than the Red Bay series and the Wood Bay series and probably equivalent to the Grey Hoek series and perhaps in part also to the Wijde Bay series.

Besides by the Norwegian expeditions, collections of Devonian fishes have in more recent time been made by Swedish expeditions in the Ice Fjord area, viz. by HÖGBOM in Mimer Valley during the summers of 1910 and 1911, by the writer in Mimer Valley during the summers of 1916 and 1917 and by Dr. E. WIRÉN and Cand. A. STENSIÖ at Mt. Lyktan during the summer of 1920.

The collections brought home by B. HÖGBOM and by myself have been partly determined and described (STENSIÖ 1918 a, pp. 68—73; 1918 b, pp. 115—122; 1923, pp. 1241—1249), and the forms which were thus added to those previously known from Mimer Valley are: *Onchus* sp., *Dictyonosteus arcticus* (Crossopterygian) and *Rhadinichthys* sp. Of these *Dictyonosteus* and *Rhadinichthys* are from the strata considered by WOODWARD to belong to the upper Devonian. In these strata I have in addition found numerous remains *Arthrodiran* jaws. The *Onchus*-species, associated with numerous remains of *Pteraspis*, Arthrodires and *Porolepis*, occur mostly in strata which have hitherto been held to be of a lower Devonian age (STENSIÖ 1918 a, p. 68).

The material of Cephalaspids on which this monograph is based, with the exception of a fragmentary piece found by NATHORST 1882, has been collected entirely by Norwegian expeditions, chiefly by those in 1909—1912 and by the one in 1925, and, as will appear from my account, it is beyond question one of the most important discoveries of fossil vertebrates ever made.

The tables below give the particulars concerning the Norwegian expeditions, and the collecting of the material described in this monograph.

The earlier Swedish collections belong to the Royal State Museum of Natural History of Stockholm. The collections brought together by B. HÖGBOM, by myself and by Dr. WIRÉN and Cand. A. STENSIÖ are in the Museum of the palaeontological institution of Uppsala, while the Norwegian collections belong to the Palaeontological Museum of Oslo.

According to the geological investigations and the examination of the fossils, the sequense of the Downtonian and Devonian strata of NW Spitsbergen is as shown by the table on p. X.

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[1] According to QUENSTEDT 1926 it is not quite excluded that this series might be somewhat older and perhaps belong to the uppermost part of the lower Devonian.

Table of the Collecting of Downtonian and Devonian fossils

by *The Norwegian Spitsbergen Expeditions.*

Year	Leader	Geologists and Collectors	Localities
1906	The expeditions fitted out by Prince Albert I of Monaco and led by G. Isachsen	Arve Staxrud	Mt. Pteraspis, between the points 760 and 825.
1907		Adolf Hoel	West side of Wood Bay, N. of Hoffnung Glacier.
1909	G. Isachsen	Adolf Hoel Olaf Holtedahl	Ben Nevis; Fränkel Ridge. The inland E. of Kings Bay (Mt. Exile, Mt. Diademe, Three Crowns); Reindeer Peninsula (the ridge between Arla and Serla Glaciers, M. Högkulla).
1910	G. Isachsen	Adolf Hoel	Around Bock Bay; the inland between Bock Bay and Monaco Glacier; around Liefde Bay; Fränkel Ridge.
		Olaf Holtedahl	East side of Wood Bay.
		G. Watnelie	Ben Nevis, the Cliff; west side of Wood Bay, N. of Hoffnung Glacier.
1911	Adolf Hoel and Arve Staxrud	Olaf Holtedahl	The inland between Wood Bay and Ekman Bay.
		Adolf Hoel and Olaf Holtedahl	Fränkel Ridge; Mt. Lyktan and the region between Dickson Bay and Wijde Bay (East Fjord).
1912	Adolf Hoel and Arve Staxrud	Adolf Hoel	Reindeer Peninsula; Mt. Pteraspis; around Liefde Bay; around Bock Bay; around Mt. Halvdan; west side of Wood Bay; N. of Hoffnung Glacier; west side of Wijde Bay.
1917	Adolf Hoel and Sverre Røvig	Adolf Hoel	Around Horn Sound.
1918	Adolf Hoel and Sverre Røvig	Adolf Hoel	Around Horn Sound.
1919	Adolf Hoel	Adolf Hoel	The inland between Horn Sound and South Cape.
1920	Adolf Hoel	Adolf Hoel	The inland between Horn Sound and South Cape.
1924	Adolf Hoel	O. Høeg	The inland between Dickson Bay and Wijde Bay (West Fjord); Mt. Lyktan.
1925	Th. Vogt	Th. Vogt and Anatol Heintz	The Land between Klaas Billen Bay and Dickson Bay; Mt. Lyktan. Fränkel Ridge; Ben Nevis; west side of Wijde Bay.

In conclusion some information is given regarding the stratigraphic position of the localities mentioned in this publication.

As before stated the *Red Bay* series is the oldest subdivision. The localities best examined are mentioned below.

In *Fränkel Ridge* are found the oldest layers in the series. The dip is towards the west so the oldest layers are found high up in the mountainside and the younger lower down.

The Collecting of the Material described in this Monograph.

Number of specimens of Cephalaspids collected from 1909 to 1925.

Collectors	1909	1910	1912	1924	1925	Total
Hoel	68	1	6			75
Holtedahl . . .	4					4
Watnelie		7				7
Høeg				2		2
Heintz					14	14
Total	72	8	6	2	14	102
	80					
Expeditions	Isachsen		Hoel and Staxrud	Hoel	Vogt	

A. G. Nathorst 1882 .	1
Collector unknown . . .	2
Total	3 + 102 = 105 specimens

The lowermost layers of the Red Bay series are also found in the lower part of *Mt. Pteraspis* on the north side of Liefde Bay.

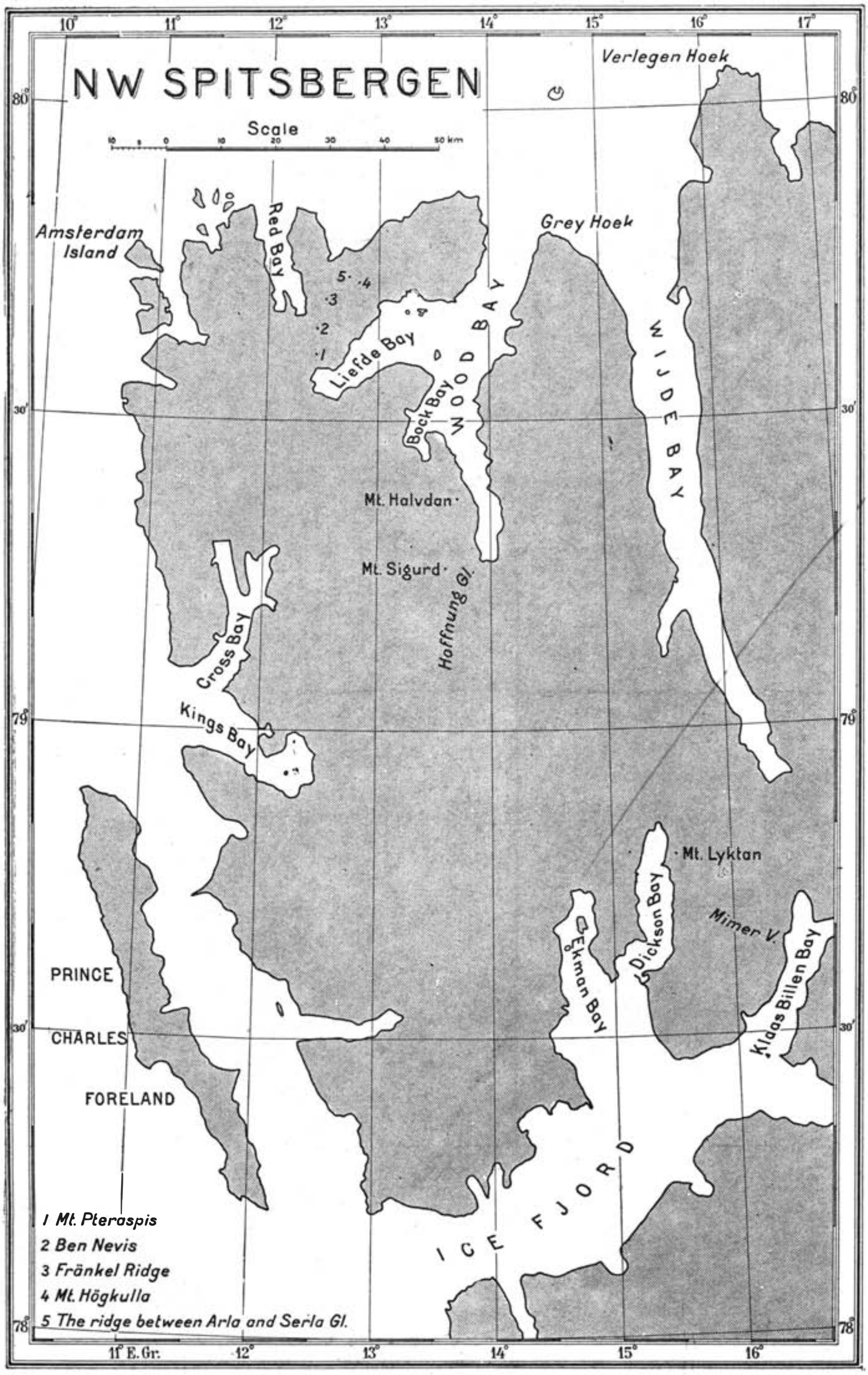
The subsequent strata are then found in the lowermost beds of *Ben Nevis*, a mountain between Red Bay and Liefde Bay, 913 m. high. In this mountain there has been traced a continuous section in which collections have been made from 22 horizons, at altitudes from 60 to 900 m. above sea level. The lowest altitudes are denoted by letters from A (60 m.) to I (170 m.). Then comes *The Cliff* with two altitudes at 260 and 290 m., respectively, and then the altitudes from J (500 m.) to U (900 m.). The lower and probably the middle part of Ben Nevis correspond to the higher parts of Mt. Pteraspis. The strata in the above mentioned mountains form a syncline, the layers in Ben Nevis being in the middle of the trough.

Collections of the *Wood Bay* series have been made at the following places:

At the left side of Hoffnung Glacier, from Mt. Sigurd to the fjord. The fossils have been found immediately above the boundary towards the Red Bay series, further at a level of 400 m. above this boundary,

The Downtonian and Devonian strata of NW Spitsbergen.

Series	Age	Nature of Rocks	Fossils	Thickness	Remarks
Wijde Bay Series	Probably Upper Devonian, but older than the Upp. Dev. Ursa sandstone (Bear Island).	Grey sandstones, grey and black shales.	Fishes, lamellibranchs, ostracodes.	About 2000 m.	Conformity
Grey Hoek Series	Uppermost Lower Devonian or lowermost Middle Devonian.	Dark grey, fine-grained shales with subordinate layers of sandstone (at the base 200 m. transition layers).	Molluscs, land plants, few fish remains.	About 2000 m.	Marine transgression. Apparent conformity.
Wood Bay Series	Lower Devonian.	Micaceous sandstones and shales, mostly red, also brown and green, rather regularly laminated, very frequently with ripple-marks (widely distributed in NW Spitsbergen as far south as Ice Fjord; as far west as Kings Bay).	Fishes, ostracoderms (abundant), ostracodes, plants.	About 3000 m.	Fauna endemic. Conformity.
Red Bay Series	Uppermost Silurian (Downtonian).	Mostly green, but also red, sandstones and shales with limy lenticles (fishes).	Ostracoderms (abundant), fishes (rare), lamellibranchs, ostracodes (Ben Nevis and upper part of Mt. Pteraspis).	About 900 m. 1500 m. About 3000 m.	
		Red and grey sandstones, in several layers containing ostracoderms.	Ostracoderms (abundant), fishes (rare), (Fränkel Ridge, and lower part of Mt. Pteraspis).	Several 100 m.	
		Yellow-white, non-fossiliferous, coarse-grained, moderately cross-bedded sandstones.		100—200 m.	
		Red, slightly bedded, conglomerates with rather small well-rounded pebbles of quartz and limestone. Breccias with sharp-edged blocks (not comminuted weathering débris of the Hecla Hoek mountain).		500—600 m.	Transgression (unconformity).
					Denudation of the Caledonian folding.
Hecla Hoek Series	Partly Ordovician (Bear Island).	Metamorphe sediments (Caledonian folding).			


NW SPITSBERGEN
Scale
10 5 0 10 20 30 40 50 km
Verlegen Hoek
Amsterdam Island
Red Bay
Grey Hoek
Liefde Bay
WOOD BAY
Bock Bay
WIJDE BAY
Mt. Halvdan
Mt. Sigurd
Hoffnung Gl.
Cross Bay
Kings Bay
Mt. Lyktan
Dickson Bay
Mimer V.
Ekman Bay
Klaas Billen Bay
PRINCE CHARLES FORELAND
ICE FJORD
1 Mt. Pteraspis
2 Ben Nevis
3 Fränkel Ridge
4 Mt. Högkulla
5 The ridge between Arla and Serla Gl.
10° 11° 12° 13° 14° 15° 16° 17°
80° 30′ 79° 30′ 78°
11° E. Gr. 12° 13° 14° 15° 16°

and at another level 1300 m. above it. The latter place has been described as the *west side of Wood Bay*, *N. of Hoffnung Glacier*, the two others as *W. of the Hoffnung Glacier.*

On the *Reindeer Peninsula* the stratigraphic boundary between the Red Bay series and the Wood Bay series is not exposed, but it is probable that the layers in which HOLTEDAHL made collections in 1909 in the *ridge between the Arla and Serla Glaciers* and at *Mt. Högkulla* belong to the lower part of this series. The level at which HOEL made collections in 1910 has a somewhat higher altitude.

The collections from the *vicinity of Mt. Halvdan* belong to the middle part of the Wood Bay series.

As the dip of the strata of the Wood Bay series everywhere is towards the east, we find the youngest layers of this series on the east side of Wood Bay.

As to the stratigraphical position of the Wood Bay layers in *Mt. Lyktan*, *east of Dickson Bay*, and in the *inland east of Kings Bay* nothing is known from the geological investigations.

For the great privilege of studying the extraordinarily valuable material of Cephalaspids described in this monograph I am highly indebted to Professor J. KIÆR of Oslo, who in the most obliging way placed it at my disposal. And further I wish to express here my deep gratitude to Professor KIÆR for the great liberty he gave me concerning the choice of methods for the researches I wished to carry out. Finally, I desire to thank Professor KIÆR most cordially for very great courtesy in other respects during my work with the Cephalaspid material and for a collaboration that has been very pleasent in all respects.

It is also a pleasure to me to acknowledge here my debt of gratitude to Professor O. HOLTEDAHL of Oslo, who during a visit to Uppsala in 1921 made me interested in the Old Red fishes from Northern Spitsbergen and who originally arranged that the scientific treatment of certain of them was entrusted to me.

In this connection I should also like to offer my most sincere thanks to Docent ADOLF HOEL of Oslo for the great help I have received from him in writing the remarks given above on the geology of the Old Red Deposits of Northern Spitsbergen. (In fact the stratigraphical remarks on pp. VIII—X have been written by Docent HOEL). And I also wish to say my best thanks to Docent HOEL for the great interest he has taken otherwise in this work.

The drawings for this work have been made by Mr. G. LILJEWALL, Mr. S. EKBLOM, Mrs. AÏNA STENSIÖ and Miss A. STARUP.

HISTORICAL

To the family *Cephalaspidae* in its modern conception are, as is well known, referred the genera *Cephalaspis* AGASSIZ, *Thyestes* EICHWALD (or *Auchenaspis* EGERTON), *Eukeraspis* LANKESTER, *Ateleaspis* KIAER and *Micraspis* KIAER. Generally the genus *Didymaspis* LANKESTER too is included in the family.

The genus *Cephalaspis* was established by AGASSIZ in 1835 (Tome II, Part 1, p. 135—152) on the basis of material collected by MURCHISON and other British geologists during the geological researches of the lower Palaeozoic formations that were undertaken at that time in England, Wales and Scotland. AGASSIZ referred to the genus four species, *C. lyelli*, *C. rostratus*, *C. lewisii* and *C. lloydii*, the three latter of which as we now know do not pertain to it but to the genus *Pteraspis*. That *C. lewisii* and *C. lloydii* were very different from his *C. lyelli*, however, was quite clear to him, and he even emphasized that these two species would probably have to be referred to a new genus when they became known more in detail. On the other hand he had no idea of that his *C. rostratus* too also went with them and not with *C. lyelli*.

In his monograph of the fishes of the Old Red Sandstone published in 1844 (p. 31) AGASSIZ still retained the four above-mentioned species in the genus *Cephalaspis* and this was also done by MURCHISON (1839, Part II pp. 587—596), PICTET (1845, p. 249; 1854, p. 220) and GIEBEL (1848, pp. XI, 259, 268—269).

The first to really perceive the great difference between *C. lyelli* on the one hand and *C. lewisii* and *C. lloydii* on the other was KNER in 1847. For the last mentioned two species he established the new genus *Pteraspis* and, contrary to AGASSIZ, he was of the opinion that these two species could not be fishes, but pertained to Cephalopods atlied to *Sepia*.

In an excellent paper published in 1858 (1858a) HUXLEY made it still more clear that the skeleton of *C. lyelli* was in certain respects very different from that in *C. lewisii* and *C. lloydii* and he adopted for the latter two species the generic name *Pteraspis* introduced by KNER. On the other hand he strongly objected to KNER's view concerning the systematic position of *Pteraspis*. "No one can, I think, hesitate", he said, (p. 277) "in placing Pteraspis among fishes. So far from its structure having 'no parallel among fishes' it has absolutely no parallel in any other division of the animal kingdom. I have never seen any Molluscan or Crustacean structure with which it could be for a moment confounded. Its relations with Cephalaspis, on the contrary, are very close." But though the difference between *Cephalaspis* and *Pteraspis* had thus been made out to a certain extent, the two genera were still for a long time considered to be closely allied to each other.

Shortly after the publication of the paper just cited HUXLEY in a notice (1858 b, pp. 82—83) showed that the species *Cephalaspis rostratus* AGASSIZ also must be referred to *Pteraspis*. And accordingly the genus *Cephalaspis* at that time was deliberated from other forms and received its modern definition.

New species have been added to *Cephalaspis* by EGERTON (1857, pp. 283—286), LANKESTER (1870), WHITEAVES (1881 p. 98; 1889 p. 92) and TRAQUAIR (1890 a, pp. 16, 21; 1893 a, 1893 b; 1893 c pp. 113—115; 1894 a; 1899 a)[1]. And a thorough revision of the species described up to 1891 was made by WOODWARD in Part II of his Catalogue of Fossil Fishes in the British Museum. A suggestion by LANKESTER in 1870 (p. 43) to divide *Cephalaspis* into three subgenera has not been adopted by subsequent writers, as it has been difficult to get an idea of the lines of variations in the genus. Finally it deserves here to be pointed out that, since the descriptions by AGASSIZ and HUXLEY, valuable contributions to the morphology of the genus *Cephalaspis* have been given especially by LANKESTER (1870), PATTEN (1903 c, pp. 827—859; 1912), JAEKEL (1903), KEMNA (1903, 1904) and WOODWARD (1906, pp. 267—270; 1920, pp. 31—33).

The genus *Thyestes* was established in 1854 by EICHWALD. His definition, however, was very incomplete. More detailed descriptions of the type species *Th. verrucosus* were later given by PANDER (1856, p. 47), EICHWALD (1860, p. 1532), SCHMIDT (1866), ROHON (1892 pp. 12—37; 80—87; 1895; 1896 a; 1896 b) and JAEKEL (1911, fig. 20, p. 35; 1921, fig. 9, p. 229). In 1894 SCHMIDT referred to *Thyestes*; the species previously known under the name of *Cephalaspis schrenki* PANDER; and further species of the genus *Thyestes* have been described by ROHON in 1892.

Three years after the genus *Thyestes* had been established the new generic name *Auchenaspis* was introduced by EGERTON (1857, p. 286). As it became known more completely, however, *Auchenaspis* appeared to be closely allied to *Thyestes*, so closely indeed that by

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[1] Cf. also the works of HARLEY (1859) and SALTER (1868, p. 240) etc.

most palaeoichthyologists it has been considered to be identical with the latter. According to the current rules of nomenclature, therefore, the generic name *Thyestes* should have to be used for it, but on account of the deficient definition originally given to it by EICHWALD this generic name has not been generally adopted (cf. WOODWARD 1891 a, p. 195; 1898, p. 11; GOODRICH 1909, p. 203; SCHMIDT 1894, pp. 204—205; ROHON 1892, pp. 80, 81, 85, 86; 1894, p. 203). We shall have the opportunity to return to this subject below in another place in this memoir.

The genus *Eukeraspis* was founded by LANKESTER in 1870 for a species which in most respects is closely allied to *Cephalaspis*. Only the type species is known so far.

The genus *Ateleaspis* was established by TRAQUAIR in 1899 (1899 c, pp. 834—837). On account of the fragmentary state of preservation of the material, TRAQUAIR was at first inclined to think that *Ateleaspis* was rather different from the other Cephalaspids known, but when new, more complete specimens were found he soon perceived that this was not the case (TRAQUAIR 1904, pp. 883—886).

The two genera *Aceraspis* and *Micraspis* were constituted by KIAER in 1911, and further contributions to the knowledge of them were given in 1924 (KIAER 1924, p. 17, figs. 8, 10). So far, however, no complete description of them has been published. *Aceraspis* is said to be without cornua and to be intermediate in its characters between *Ateleaspis* and *Cephalaspis*. *Micraspis* is also said to lack cornua but in other respects to resemble *Cephalaspis* most closely.

Finally the genus *Didymaspis* was founded by LANKESTER in 1867 (p. 152). LANKESTER recognized its affinities with *Thyestes (Auchenaspis)* and *Cephalaspis*, and placed it with these genera in the family *Cephalaspidae* (cf. also LANKESTER 1870, pp. 59—60). His view in this respect has been accepted by most palaeoichthyologists such as WOODWARD (1891 a, p. 199), ZITTEL (1887, p. 150), KOKEN (1911, p. 34), SCHLOSSER (1918, p. 34; 1923, p. 35), ABEL (1919, p. 78), GOODRICH (1909, p. 204) etc. Another view — that *Didymaspis*, on the contrary, is to be referred to the family *Trematаspidae* — was advanced by ROHON (1894, pp. 204, 221—222; 1896 a, pp. 15, 29) and adopted by ZITTEL in 1895 (p. 554). Now if it really was so that *Didymaspis*, as is generally maintained, lacks cornua it would undoubtedly be very similar to *Tremataspis* and ROHON's view should perhaps be accepted. But since, as I have found (text.fig. 80), it has distinct, though short cornua it seems in this respect to occupy an intermediate position between the families *Cephalaspidae* and *Trematаspidae*.

In this connection it deserves also to be mentioned that the genus *Tremataspis* SCHMIDT was for a long time associated with the *Cephalaspidae* to which it is beyond question closely related. As it differs in certain respects, however, from the genera referred to the *Cephalaspidae* WOODWARD established for it in 1891 an independent family, *Tremataspidae*, and this procedure of WOODWARD'S has since been adopted by subsequent writers almost without exception. It is also to be added here that *Trematаspis*, owing to a generally good state of preservation, has been more studied and that up till now it has also been better known in detail than any of the genera of the family *Cephalaspidae*. The most important contributions to the knowledge of it have been published by SCHMIDT (1866, pp. 19—32), ROHON (1892, pp. 37—82), PATTEN (1903 a; 1912 etc.), WIMAN (1918, pp. 86—95) and JAEKEL (1921, pp. 235—239).

As one of the oldest known groups of vertebrated the Cephalaspids have ever since their discovery attracted much interest. Despite this, however, our knowledge of their anatomy remained for a long time very slight since the state of preservation in which their representatives were found was generally very imperfect. The features on which most of the previous palaeoichthyologists had to base their opinions concerning the relationships and systematic position of the Cephalaspids were therefore very limited and at least for a long time at first not likely to lead to a true apprehension. When this fact is realised, it will not be surprising that the opinions advanced concerning the relationships of the Cephalaspids are both numerous and widely different.

The fragmentary specimens of Cephalaspids first discovered were for some time considered to be remains of trilobites. LONSDALE, however, soon arrived at the conclusion that they pertained to fishes (MURCHISON 1839, Part II, p. 587); and as AGASSIZ at that time was working on his "Récherches", they were submitted to him for a closer investigation, probably in 1834.

Already in 1835 AGASSIZ published his description of them (AGASSIZ, 1835 Récherches sur les poissons fossiles, Tome II, Part 1, pp. 135—152). In that he declared that they must be fishes and, as already pointed out above, he established for them the genus *Cephalaspis* which he placed in his family *Lepidoides*,[1] accordingly among the ganoids. In 1844 he associated *Cephalaspis* with *Pterichthys*, *Pamphractus*,[2] *Polyphractus*,[3] *Coccosteus* and *Chelonichthys*[4] in a family

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[1] This family comprised, besides *Cephalaspis*, genera as among others: *Coccosteus*, *Chelonichthys*, *Cheirolepis*, *Cheiracanthus*, *Diplacanthus*, *Acanthodes*, *Dipterus*, *Osteolepis*, *Palaeoniscus*, *Catopterus*, *Coccolepis*, *Eurynotus*, *Platysomus*, *Gyrolepis*, *Plectrolepis*, *Dapedius*, *Tetragonolepis* and *Amblyurus*. It was thus a very heterogenous family.

[2] Synonym of *Bothriolepis* (cf. WOODWARD 1891 a, p. 231).

[3] Synonym of *Dipterus* (cf. WOODWARD 1891 a, pp. 235—236).

[4] Synonym in part of *Asterolepis*, in part of *Heterosteus* (cf. WOODWARD 1891 a, pp. 203, 308).

which he named *Cephalaspides* (AGASSIZ 1844, Recherches sur les poissons fossiles, T. I, p. XXXIII, tableau general; 1844 monograph poissons vieux grès rouge, pp. 1—5, 157). Concerning the relationships of that family he expressed himself as follows (Monograph poissons vieux grès rouge p. 4): "Si nous recherchons maintenant les affinités naturelles que présente cette famille, nous trouverons qu'elle se rapproche, d'un côté, des Esturgeon, de l'autre, des Goniodontes et des Siluroides cuirassés. Cependant les affinités avec les Loricaires se bornent aux plaques osseuses et émaillées; le squelette et la disposition même des plaques sont fort différents. L'analogie est bien plus frappant avec les Esturgeons, à raison de la persistance de la corde dorsale, du développement retardé de tout le système osseux, qui n'entre pas en relation avec la peau, et de la formation de plaques cutanées, couvertes d'émail. Mais d'un autre côté, la structure et la position de la bouche, et le développement des nageoires paires et impaires, sont si différents dans ces deux familles, que tout en reconnaissant leur affinité, il sera toujours impossible de les réunir."

"La famille des Céphalaspides constitue par conséquent un type à part dans la règne animal, comme dans l'histoire du développement des poissons, puisque d'un côté ses caractères zoologiques sont nettement tranchés, et que de l'autre sa présence est restreinte au seul terrain du vieux grès rouge."

PICTET in 1845 (pp. 248—251) adopted the family *Cephalaspides* with the conception given to it by AGASSIZ and referred it — together with the families *Lepidoides*, *Acanthodes*, *Dipteriens*, *Sauroides*, *Coelacanthes*, *Pycnodontes*, *Sclerodermes*, *Gymnodontes*, *Lophobranches* and *Acipenserides* — to the ganoids. He also considered at that time like AGASSIZ the true affinities of the family to be with the sturgeons and with the armoured Siluroids.

About a decade later (1854), however, PICTET had modified his views from 1845 to some extent. He was not able to maintain any longer that the Cephalaspids had affinities to the Siluroids but was now still more convinced of their close relationships with the sturgeons and Polyodontids. He associated them with these in an order which he named Ganoides cuirrassés. It deserves further to be mentioned here that in 1854 he added to the Cephalaspids the genus *Menaspis* which had been constituted by EWALD in 1848 and which was supposed by this writer to be related to the Cephalaspids. GIEBEL in 1848 (pp. 259—280), like PICTET, accepted the family *Cephalaspides* of AGASSIZ's definition, and, like PICTET and AGASSIZ too, he referred it to the Ganoids. Among these he associated it with the families *Acipenserini* and *Holopthychii* in his order *Chondrostei.*

M'COY, on the contrary, in a paper published in 1848 restricted the family *Cephalaspides* so as to comprise only the genus *Cephalaspis.*

For the other genera referred by AGASSIZ to the famly *Cephalspides* he constituted a new family which he named *Placodermi.* M'COY thus was the first to perceive the very heterogenous character of the family *Cephalspides* in its original conception and to undertake a revision of it.

QUENSTEDT in the first edition of his well-known "Handbuch" in 1852 (pp. 231—232) had probably overlooked the paper by M'COY referred to just above, as he did not mention it and as in addition he referred to the family *Cephalaspides* the same genera as AGASSIZ. The family *Cephalaspides* was described in connection with the *Coelacanths* the *Sclerodermns*, the *Gymnodonts*, the *Lophobranchs* and the *Acipenserids* in an "Anhang zu den Ganoiden", and he called attention to the fact that all these fishes were very different from true ganoids with regard to the dermal skeleton (p. 228).

PANDER in 1856 (pp. 46—47) accepted the Cephalaspids with the conception proposed by M'COY. In the following year he published his monograph on the Placoderms of the Devonian system (1857), which certainly helped greatly towards a better understanding of the difference between the various forms included by AGASSIZ among his *Cephalaspides* and accordingly formed a support for the classification proposed by M'COY.

HUXLEY in 1858 (1858a) in connection with his reserches on the microscopic structure of the shields of *Cephalaspis* and *Pteraspis* also entered upon the question of the zoological position of the Cephalaspids, to which, if I understand him right, he referred not only the two genera just mentioned but also *Pterichthys* and *Coccosteus.* He compared the Cephalaspids to Siluroids and Acipenserids, but did not consider that he could place them with these. The only conclusion he believed he could arrive at was that *Pteraspis* and *Cephalaspis* must be either Ganoids or Teleosts; "but", he added, "to which of these orders they belong, there is no evidence to show" (p. 279).

A few years later HUXLEY wrote concerning *Pteraspis* as follows (1861 a, p. 166): "It is not easy to find an exact parallel for such a cephalic covering as this among existing fishes. *Loricaria*, *Tetrodon naritus*, *Acipenser* and *Spatularia* seem to present the nearest analogies, — the two former being much more remote than the two latter. In fact if the bony cephalic shield of the Acipenseroid fishes were ossified in one piece, it would very closely resemble that of both *Cephalaspis* and *Pteraspis*, and would hardly differ more from either than the two from one another."

In his "Essay on the systematic arrangement of the fishes of the Devonian epoch", published in 1861 (1861 b), HUXLEY referred to the Cephalaspid family for wich he now proposed the name *Cephalaspidae* the genera *Cephalaspis*, *Pteraspis*, *Auchenaspis* and *Menaspis. Thyestes*, on the contrary, he did not mention, although it had been placed among the Cephalaspids both by EICHWALD in 1854 (p. 109) and PANDER in 1856 (pp. 44—47). *Coccosteus* and *Pterichthys* and their allies he removed entirely from the *Cephalaspidae.* Concerning the systematic position of the *Cephalaspidae* he had at this time advanced to a more decided opinion than earlier, since he now placed them provisionally among the *Chondrostei* (p. 38).

EGERTON in 1860 (p. 127) accepted M'COY'S subdivision of the Agassizian family of Cephalaspids into *Placodermi* and *Cephalaspides* proper and considered the latter to consist of the genera *Cephalaspis*, *Pteraspis* and *Auchenaspis.* The same view was also advanced later by SCHMIDT in 1866 (pp. 29—32), who referred to the family *Cephalaspidae* the genera *Cephalaspis*, *Tremataspis*, *Auchenaspis*, *Thyestes* and *Pteraspis.* *Pteraspis,* however, he said, was rather different from the others. Seven years later (1873, p. 138) he still more emphasized that difference and expressed the opinion that *Pteraspis* could not pertain to the family *Cephalaspidae.* BRANDT in 1866 (pp. 43—48) in fact also accepted M'COY'S subdivision of the armoured palaeozoic "fish" forms, although he proposed, instead of *Placodermi*, the name *Arthrothoraces* and, instead of *Cephalaspidae*, the name *Aspidocephali.* To the latter, however, he referred not only *Cephalaspis*, but also *Menaspis.* Like HUXLEY in 1861 he was of the opinion that the *Arthrothoraces* and *Aspidocephali* were allied to sturgeons.

QUENSTEDT in the second edition of his "Handbuch" published in 1867, despite M'COY'S and HUXLEY'S revisions of the Cephalaspids and the progress in the knowledge of the fossil fishes since the appearance of the first edition, still retained the Cephalaspids with the old conception given by AGASSIZ, although he adopted the genera *Pteraspis* and *Thyestes* and added *Menaspis.* His Cephalaspids were now placed among his heterocercal ganoids together with *Palaeoniscus*, *Amblypterus*, *Pygopterus*, *Platysomus Megalichthys*, "the *Dipterini* of the Old Red", the genus *Holopthychius,* the *Sclerodermi*, the *Gymnodonti*, the *Lophobranchii*, the Acipenserids and certain other forms. It may also be pointed out here that QUENSTEDT now dealt with the Coelolepid scales and the Conodonts in connection with the Cephalaspids.

A new and still more thorough revision of the family *Cephalaspidae* than those by M'COY and HUXLEY was made in 1868—1870 by LANKESTER in his excellent monograph of the Fishes of the Old Red Sandstone. LANKESTER in that work, after removing *Menaspis* as a genus of uncertain position, divided the family into two divisions, the *Heterostraci* and the *Osteostraci.* To the *Heterostraci* he referred *Pteraspis* and its allies, to the *Osteostraci*, the genera *Cephalaspis*, *Eukeraspis*, *Auchenaspis*, *Thyestes* and *Didymaspis.* The fact that *Tremataspis* was not mentioned seems to be due to the circumstance that he probably did not know SCHMIDT'S paper on that genus, published four years earlier.

While in the beginning of his monograph (1867, p. 13) he did not seem to doubt that the *Heterostraci* and *Osteostraci*, despite the structural differences between them were closely allied to each other, he had obviously greatly changed his view on this subject in the remarks he added after the description of *Didymaspis* (1870, p. 62). "The *Heterostraci*", he there said, "are associated at present with the *Osteostraci* because they are found in the same beds, because they have, like *Cephalaspis*, a large head-shield, and because there is nothing else with which to associate them. There is at present no evidence that the body and fins of *Pteraspis* and its allies were like those of *Cephalaspis*, and the shields are not so closely similar in plan, much less in histological structure, as to warrant any inference of similarity in other parts." He thus suspected very strongly that the *Heterostraci* and *Osteostraci* really were not very closely related, and their association in one family was obviously meant to be only provisional.

With regard to the systematic position of the *Heterostraci* and *Osteostraci* LANKESTER in 1868 (p. 13) accepted the views advanced by HUXLEY in 1861 and accordingly placed them provisionally among the *Chondrostei*. In 1870 (pp. 61—62), on the contrary, he was very much in doubt as to which forms among amphirhine fishes he should relate them. That they could be allied to lampreys he was not at all inclined to believe.

LÜTKEN in 1873 (pp. 41—43) dealt with the Cephalaspids together with the other armoured Palaeozoic fishes under the common term of "Panzer Ganoiden" or "Placoderms", thus using the latter term in a meaning very different from the original one. In his opinion, the researches up to that time had failed to determine the relationships of the "Placoderms" with other fishes. He therefore considered that he could not give them any definite position in the system, but classified them as *Incertae saedis.*

TRAQUAIR in 1877 (p. 9) also held a similar view concerning the systematic position of the *Cephalaspidae* and *Placodermi*, both of which were given by him in the original conception proposed by M'COY.

QUENSTEDT in 1882, in the 3rd edition of his "Handbuch", still referred to the Cephalaspids the same forms as in 1867, adding, however the genus *Tremataspis.* His wiew concerning the relationsships of the Cephalaspids was also the same as in 1867.

As has been pointed out, LANKESTER in 1870 and SCHMIDT in 1873 had strongly emphasized the difference between the *Heterostraci* and *Osteostraci*; and the latter scientist had even expressed the opinion that the *Heterostraci* and *Osteostraci* could not pertain to one family. To ZITTEL in 1887 (p. 147) the difference between these two groups also seemed of much taxonomic importance, and he therefore gave them the rank of orders. For the two orders thus established he did not, however, accept the names introduced by LANKESTER, but proposed, instead of *Heterostraci*, the name *Pteraspidae* and, instead of *Osteostraci*, the name *Cephalaspidae.* To the latter he referred the genera *Cephalaspis*, *Auchenaspis*, *Eukeraspis*, *Thyestes*, *Didymaspis* and *Tremataspis* in the order here enumerated without grouping them into familes. *Menaspis* was excluded from them as a form the relationships of which could not be established. Both the order *Heterostraci* and the order *Osteostraci* were placed with the ganoids, but concerning the latter, the *Placodermi* and the *Acanthodi* he said (p. 144) that they occupied "eine zweifelhafte Mittelstellung zwischen Selachiern, *Chondrostei* und Knochenfischen."

COPE in 1889 (pp. 852—853) associated the Pteraspids, Cephalaspids and Pterichthyids (*Antiarchi*) in a unit which he called *Ostracodermi.* The *Ostracodermi* thus defined he placed with the *Cyclostomes* in a class of Craniates, for which he proposed the name *Agnatha.* And as the most important characteristics of that class, which was considered equivalent to *Pisces*, *Batrachia*, etc. he emphasized the absence of the lower jaw, the absence of the pectoral arch and the absence of an ossified internal skeleton. COPE thus introduced an entirely new opinion concerning the affinites of the Ostracoderms.

WOODWARD in 1891 (1891 a, pp. XVII—XVIII) adopted the term *Ostracodermi* introduced by COPE as a common name for the *Heterostraci*, *Osteostraci* and *Antiarchi*, which all were given the rank of orders. Among the *Osteostraci* he established two families — one, *Tremataspidae*, for *Tremataspis*, the other, *Cephalaspidae*, for all the other Cephalaspids. The *Ostracodermi* he placed as a sub-class of fishes, objecting to both COPE'S and PATTEN'S views, and sumarizing his views as follows (p. XVIII): "In short, all positive characters are rather in favour of an alliance with the class Pisces than otherwise; and although these organisms cannot be defined with scientific precision, it seems advisable at present to regard them as a primitive Piscine sub-class of uncertain affinities."

ROHON in 1892 (pp. 82—88) accepted the names *Heterostraci* and *Osteostraci.* Contrary to WOODWARD, he divided the *Osteostraci* into three families: *Thyestidae*, with *Thyestes*; *Tremataspidae*, with *Tremataspis*; and *Cephalaspidae*, with *Cephalaspis*, *Auchenaspis*, *Didymaspis*, and *Eukeraspis.* That at that time he placed *Thyestes* and *Auchenaspis* in different families was due to the fact that he had not perceived the close relationships between them. The *Heterostraci* and *Osteostraci* he associated in a sub-class of fishes, to which he gave the name *Protocephali.* Two years later (1894, pp. 203, 204, 221—222) he removed

Didymaspis from the *Cephalaspidae* and referred it to the *Tremataspidae*. In 1896 (1896 a) he proposed for the *Heterostraci* the new name *Aspidorhini*, whereas the *Osteostraci* were termed *Aspidocephali*. The subdivision of the latter into the same three families as in 1892 was retained, but to the *Tremataspidae* he now added the doubtfull *Oonaspis*, described by JAHN in 1894 (p. 381).

The names *Pteraspidae* and *Cephalaspidae* used by ZITTEL in 1887 for the orders *Heterostraci* and *Osteostraci* had in 1887 been objected to by COPE (1887, p. 1015) because of their family endings, and ZITTEL therefore in 1895 readopted *Heterostraci*, whereas instead of *Cephalaspidae* he chose for the *Osteostraci* the name *Aspidocephali*. *Aspidocephali* had, however, been introduced by BRANDT in 1866 for both *Pteraspis* and *Cephalaspis* and their allies, thus for both the *Heterostraci* and *Osteostraci* known up to that time, and accordingly it was not as propriate as *Osteostraci*, which in addition had the priority. The reason why ZITTEL preferred *Aspidocephali* to *Osteostraci* seems therefore in fact difficult to understand. Like WOODWARD in 1891, he subdivided the *Aspidocephali* into two families: *Cephalaspidae* — in which he placed the genera *Cephalaspis*, *Eukeraspis*, *Thyestes (Auchenaspis)* — and *Tremataspidae*, to which he referred the genera *Tremataspis* and *Didymaspis*. The *Heterostraci*, *Aspidocephali*, *Antiarchi* and *Arthrodira* he now, like LÜTKEN in 1873, associated in a group which he called *Placodermi*, thus using that name with a conception very different from the original one of M'COY. The *Placodermi* thus defined he gave the rank of a sub-class among the *Pisces*, a sub-class equivalent to the sub-classes *Selachii*, *Dipnoi*, *Ganoidei* and *Teleostei*. But he emphasized the fact that this was a provisional arrangement, since the systematic position of the "Placoderms" in reality was uncertain. Finally, it may be pointed out here that in 1891 an important paper had been published by JAEKEL on *Menaspis*, and that it was shown in that paper that *Menaspis* had no relations whatever to the *Osteostraci* but that it mostly resembled certain Elasmobranchs.

DEAN in 1895 (p. 8) associated the lampreys the hags, *Palaespondylus* and the Ostracoderms — which last he gave the same conception as COPE and WOODWARD — into a separate class of vertebrates which he called *Marsipobranchi*. Thus, like COPE, DEAN considered the that Ostracoderms occupied a very low position among the vertebrates and that they must be entirely separated from the true fishes.

WOODWARD in 1897 (p. 379) had also accepted COPE's views concerning the affinities of the Ostracoderms and in his excellent "Outlines of Vertebrate Palaeontology", published in 1898, he gave (p. 1) the following classification in accordance with that point of view:

Class: *Agnatha.*
Sub-class 1 *Cyclostomi.*
Sub-class 2 *Ostracodermi.*
Order a *Heterostraci.*
„ b *Osteostraci.*
„ c *Antiarchi.*

LANKESTER in 1897 (pp. 45—47) strongly objected to the opinions that the Ostracoderms were related to Cyclostomes and also in other points he retained the same opinions as in 1870. Thus he laid much stress upon the difference between *Cephalaspis* and *Pteraspis*, and he also denied every relationship between either of these and *Pterichtys*. "There is absolutely", he said, "no reason for regarding *Cephalaspis* as allied to *Pteraspis* beyond that the two genera occur in the same rocks and still less for concluding that either has any connection with *Pterichthys*." The *Heterostraci*, *Osteostraci* and *Antiarchi* might in his opinion be considered, as a group of primitive fish-like forms "concerning the closer relationships of which judgement must be suspended."

TRAQUAIR in 1899 (1899 c) established for the new genus *Ateleaspis* a new family *Ateleaspidae*, which was considered to differ in certain important respects from the other families among the *Osteostraci*. Five years later (1904), when new and more complete material of *Ateleaspis* had been found, however, TRAQUAIR perceived that this genus was in fact so closely allied to *Cephalaspis* that he saw no necessity to retain any longer a separate family for it.

TRAQUAIR'S works in 1899 (1899 a; b; c) and 1904 were of especial importance for the knowledge and understanding of the Ostracoderms. In those works he described not only such an interesting Cephalaspid as *Ateleaspis* but also many new important forms of *Heterostraci* and new forms which pertained to a quite new order of Ostracoderms, an order which was named *Anaspida*. The observations made on this new material led TRAQUAIR to consider the *Heterostraci* and *Osteostraci* as related to each other, and thus in this point he arrived at an opinion quite opposite to that advanced by LANKESTER. As will be shown in the present work, there are now additional reasons to believe that he was right in that. Being struck by the peculiar Elasmobranch-like strukture of the dermal skeleton in certain of the *Heterostraci* he believed (1899 b, p. 602; 1899 c, p, 855) the Ostracoderms to have evolved from the Elasmobranchian stem or from common ancestors with the primitive Elasmobranchs.

DEAN in 1900 (p. 22) gave the following classification in which he separated the groups comprising the Ostracoderms, the Arthrodires and the *Cycliae (Palaeospondylus)* from those comprising other fossil and recent forms:

Chordata.

Class *Ostracophari* COPE 1891 (= Ostracodermi, COPE 1889).
Sub-class *Osteostraci.*
Sub-class *Heterostraci.*
Sub-class *Antiarcha.*
Class *Artrognathi* DEAN 1899.
Sub-class *Anarthrodira* DEAN 1899.
Sub-class *Arthrodira.*
Class *Cycliae (Palaeospondylus)* GILL 1896.
Class *Protochordata* BALFOUR 1882.
Class *Marsipobranchii.*
Class *Pisces.*

DOLLO in 1903 (pp. 700—701) considered it most probable that the Ostracoderms were agnathous vertebrates.

KEMNA in 1903 and 1904 gave a critical review of the works published up to that time especially by TRAQUAIR. He called attention to the fact that despite TRAQUAIR'S statements to the contrary there nevertheless existed several points of agreement between the Ostracoderms and the Cyclostomes, the former of which he accepted with the conception of COPE and WOODWARD. Like COPE and WOODWARD he also associated the Ostracoderms and Cyclostomes in a class *Agnatha* (1903, p. 347).

BRIDGE in 1904 (pp. 522—532) excluded the *Antiarchi* from the Ostracoderms, the relationships of which he considered it impossible to settle on the facts known up to that time.

REGAN in 1904 (pp. 340—346) associated, under the name of *Placodermi*, the *Osteosraci*, the *Antiarchi* and the *Arthrodira*, whereas the *Heterostraci* were considered to pertain to the "*Chondropterygii*". Concerning the relationships between the *Osteostraci*, *Antiarchi* and the *Arthrodires* he said: "In fact the evidence that the Coccosteidae are Teleostomi, that the Asterolepidae are allied to the Coccosteidae and that the Cephalaspidae have been derived — through the Tremataspidae — from the Asterolepidae, is so clear, that I am compelled to regard the Atelaspid structure as a modification of that of the Cephalaspid." It deserves further to be added here that concerning his *Placodermi* he expressed the opinion that they "may probably be regarded as primitive *Crossopterygii*."

GOODRICH in 1909 (pp. 195—209) introduced, instead of *Heterostraci*, the name *Pteraspidomorphi*, instead of *Osteostraci*, the name *Cephalaspidomorphi*, and, instead of *Antarchi*, the name *Pterichthymorphi*. His classification, so far as the Ostracoderms are concerned, was as follows:

Vertebrata.

Branch I *Cyclostomata.*
Branch II *Gnathostomata.*
Grade I *Pisces.*
Sub-grade 1 *Chondrichthyes* (Elasmobranchs etc.).
Sub-grade 2 *Ostracodermi.*
Order 1 *Pteraspidomorphi.*
Families: *Coelolepidae, Drepanaspidae, Psammosteidae, Pteraspidae.*
Order 2 *Cephalaspidomorphi.*
Families: *Ateleaspidae, Cephalaspidae, Tremataspidae.*
Order 3 *Anaspida.*
Order 4 *Pterichthyomorphi.*
Sub-grade 3 *Osteichthyes.*

GOODRICH was of the opinion that the *Ostracodermi*, with the general conception as given by him, could be considered only as a provisional group. He was mostly inclined to accept the opinions advanced by TRAQUAIR of certain affinities between the *Pteraspidomorphi* and the *Elasmobranchii*, but on the other hand he also found certain resemblances between the *Cephalaspidomorphi* and the forms he grouped under the name of *Osteichtyes.*

KOKEN in 1911 (pp. 24—27) adopted the subdivision of the *Osteosteraci* into two families: *Cephalaspidae* and *Tremataspidae.* He grouped under the name of *Placodermi* the orders *Anaspida, Heterostraci, Osteostraci* and *Antiarchi*, thus using *Placodermi* in a third conception different from both M'COY's and the one proposed by LÜTKEN and ZITTEL. In his opinion there were no characters which definitely pointed towards an affinity between the *Cyclostomes* and the *Placodermi* in his conception and therefore, like ZITTEL in 1895, he placed the latter as a sub-class of the class *Pisces.*

JAEKEL in 1911 in his work "Die Wirbeltiere" gave the following classification:

"Stamm" *Pisces.*

Class A *Malacostoma.*
Sub-class 1 *Paloeostraci.*
Order a *Heterostraci.*
Suborder 1 *Paleaspidi.*
Suborder 2 *Pteraspidi.*
Order b *Goniaspidi.*
Suborder 1 *Tremataspidi.*
Suborder 2 *Cepalaspidi.*
Suborder 3 *Drepanaspidi.*
Suborder 4 *Thelodonti (Thelodus, Lanarkia).*

        Order c *Anaspidi.*
        Order d *Pterichthyi* (called "Nebenordnung" on p. 37).
    Sub-class 2 *Cyclostomata.*
    Sub-class 3 *Leptocardia.*

Class B *Hypostomata.*
    Sub-class 1 *Placodermata* (Arthrodires).
    Sub-class 2 *Chondrostei.*
    Sub-class 3 *Placodea* (Elasmobranchs)

Class C *Teleostomata.*

He thus associated the *Ostracodermi* and *Cyclostomata* in a large group *Malacostoma* and pointed out that he did this because of a number of primitive features which they were said to have in common. Basing his account on his well-known theory that the fishes were derived from terrestrial vertebrates, and thus secondarily adapted for swimming, he was of course forced to the conclusion that the absence of paired fins in his *Malacostoma* was a secondary phenomenon. To him, moreover, from this point of view it was a quite natural fact that the fossil representatives of his *Malacostoma* — his *Palaeostraci* — should have a well developed hard skeleton. As will be clear from the present work there are several facts which seem to show that JAEKEL was right inasmuch as the Ostracoderms and Cyclostomes really were closely allied to each other and the ancestors of the Cyclostomes thus really had a hard skeleton.

STROMER in 1912 (pp. 36—39) considered it still impossible to relate the *Ostracodermi* to other forms known. He subdivided the *Ostracodermi* into three suborders: the *Heterostraci* (with the *Pteraspidae*), the *Osteostraci* (with the *Cephalaspidae* and *Tremataspidae*) and the *Antiarchi.*

SCHLOSSER in 1918 (pp. 26—38) adopted the same classification and the same terminology as KOKEN in 1911, thus associating under the name of *Placodermi* the orders *Anaspida*, *Heterostraci*, *Osteostraci* and *Antiarchi.* He was, however, (p. 26) inclined to think that, instead of *Placodermi*, the name *Ostracodermi* introduced by COPE and WOODWARD would be the most propriate one for all extensively armoured forms — "die eigentlichen Panserfische", as he expressed it. He added also other remarks on the *Placodermi*, the following of wich may be of interest: "Es soll nicht verschwiegen werden, daß in dieser Unterklasse *(Placodermi)* sehr heterogene Formen vereinigt sind, denn in den *Anaspiden* und *Pterolepiden* haben wir möglicherweise die Ahnen der Ganoiden und in den *Coelolepiden* und *Gemündeniden* Vorläufer von Elasmobranchiern vor uns. Wenn die Unterklasse der Placodermi hier trotzdem beibehalten wurde, so geschah es nur deshalb, wei ein so eingebürgerter Name nicht durch einen neuen Namen ersetzt werden sollte, soferne dadurch nicht eine wesentliche Verbesserung erreicht wird." Inasmuch as this refers to the retaining of the name *Placodermi* it is rather strange, since as is obvious from what has been pointed out above that name was used by him in a sense quite different from its original one. In accordance with Jaekel in 1911, he considered it probable that his *Placodermi* had a suctorial mouth and otherwise he emphasized the lack of paired fins as a very important character for them. In 1923 he still adhered to the same classification and the same opinions as in 1918.

Abel in 1919 united the *Heterostraci* and *Osteostraci* in a single unit, which he named *Osteostraci*. The *Osteostraci*, as thus defined, and the *Anaspida* he gave the rank of a sub-classes and referred both of them to the class *Pisces*.

Woodward in 1920 (pp. 25—33) made several important remarks on the *Osteostraci* and retained the conception of the Ostracoderms given by Cope.

Jordan in 1923 (pp. 81—87) gave the following classification of the lower vertebrates.

Class A *Leptocardii.*
Class B *Marsipobranchii.*
Class C *Ostracophori.*
  Order 1 *Heterostraci.*
  Order 2 *Osteostraci.*
    Families: *Cephalaspidae, Ateleaspidae, Thyestidae (Thyestes, Didymaspis, Eukeraspis, Menaspis) Odontodontidae, (Tremataspis), Euphaneropidae (Euphanerops).*
  Order 3 *Antiarcha.*
  Order 4 *Anaspida.*
  Order 5 *Cycliae* (Palaeaspondylus).
Class D *Arthrodira.*
Class E *Elasmobranchii.*
Class F *Pisces* (= Teleostomi, Osteichthyes).

Jordan (p. 84), however, felt very uncertain as to the affinities of his class *Ostracophori* and is not even convinced that the five orders he referred to it really pertain there. "It may be," he said "that the *Antiarcha* are sharks or else *Arthrodires*, that the group itself is a mailed variant of the Lampreys, that it is ancestral to the sharks, that it is derived from primitive sharks or that it is a variant of primitive crustaceans."

Kiaer in his excellent paper of the Norwegian *Anaspida* in 1924 showed the very interesting fact that there are several agreements between the *Anaspida* and the *Osteostraci* and that probably they are closely related to each other. In addition he was able to show that the *Anaspida* and *Osteostraci* had still more features in common with the Cyclostomes than had been known previously, and that they therefore undoubtedly must be considered as allied to each other. He laid especial stress on their monorhiny, which led him to the conclusion that they could not have any relationships with the probably amphirhinal *Heterostraci,* which, with TRAQUAIR, he considered to be a primitive group related to Elasmobranchs. As probably being amphirhinal, the Arthrodires too were considered to have nothing in common with the *Anaspida*, *Osteostraci* and *Cyclostomata.* His classification is as follows:

Branch I. *Monorhina* HAECKEL.

Class 1 *Anaspida.*
Class 2 *Cephalaspidomorphi.*
Class 3 *Cyclostomata.*

While the scientists dealt with above all have regarded the Ostracoderms as true vertebrates, GASKELL and PATTEN, on the contrary, have tried to relate them more or less intimatelly with Arthropods. GASKELL (1889 a; 1889 b; 1890; 1898—1906; 1908) believed the vertebrates to have evolved from a group of Arthropods including Trilobites, scorpions and Limulids, a group wich he called *Palaeostraca* (1908), and the Cephalaspids were held to be the connecting forms between the *Palaeostraca* and the Cyclostomes. He supposed that the larval Cephalaspid was an Eurypterid (1900, p. 577), and that the *Ammocoetes* was a Cephalaspid, (1900, p. 586). PATTEN (for the literature see PATTEN 1912, pp. XX—XXI) considered the vertebrates to have descended from the arachnid division of the Arthropodes, in which he included the typical Arachnids, the Trilobites and the Merostomes. He too held the Ostracoderms to be a sort of transitional forms between Arthropods and true vertebrates, but he laid much more stress on this opinion than GASKELL, a condition which caused him to create for the Ostracoderms an independent class *Peltocephalata,* which he placed between the arachnids and the vertebrates. Concerning the Cyclostomes he expressed in 1912 (p. 383; cf. also diagram p. 382) the highly interesting view that these represented one of the earliest offshoots of the Ostracoderms.

GEOLOGICAL RANGE AND GEOGRAPHICAL DISTRIBUTION OF THE CEPHALASPIDS

No representatives of the *Cephalaspidae* have yet been found with full certainty in deposits older than the upper Silurian. Since, according to the knowledge we now posses of them from the Spitsbergen forms described below, the *Cephalaspidae* attained their greatest degree of flourishing already in the upper Silurian, however, it is beyond question that they must have arisen much earlier, probably even in the Ordovician. Towards the middle of the Devonian they rapidly decreased in abundance and during the later half of that epoch they were rare. They probably became extinct before the beginning of the Carboniferous period.

As far as is known, the *Cephalaspidae* are in their geographical distribution almost exclusively limited to deposits of Europe and eastern Canada, only a single doubtfull specimen having been recorded from Australia (CHAPMAN 1906, pp. 93—100). In Europe representatives of them have been found on the Island of Oesel, Esthonia, (upper Silurian); in Scania, in the south of Sweden (upper Silurian)[1]; in the Oslo (Kristiania) area, in Norway (upper Silurian); in Scotland (upper Silurian, lower Devonian, middle Devonian); in England (upper Silurian, lower Devonian) and in the north of France (lower Devonian; LERICHE 1906, pp. 37—39). To these European localities Spitsbergen is now to be added as the most important one, the number of species found there amounting to not less than at least 24, 14 of which are from the upper Silurian, 10 from the lower Devonian. In eastern Canada Cephalaspids have been found at Gaspé (lower Devonian), at Campbellton (lower Devonian) and at Scaumenac Bay (upper Devonian. See TRAQUAIR 1890 a, pp. 16, 21 and PATTEN 1912, fig. 237 on p. 357).

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[1] Discovered by the author in 1924.

DESCRIPTION OF THE SPITSBERGEN FORMS

Material and methods.

The material of Cephalspids now available from the Red Bay series (Downtonian) and Wood Bay series (lower Devonian) of Spitsbergen consists, as a rule, merely of cephalic shields or detached fragments of such shields. No remains of the fins are known, and parts of the squamation of the trunk have been found associated with the cephalic shield only in one case (in *Cephalaspis staxrudi*). The state of preservation thus indicates that a complete decomposition of the soft tissues must generally have taken place before the specimens became embedded in the rock.

The rocks containing the Cephalaspids consist both in the Wood Bay series and in the Red Bay series of more or less coarse sandstones and conglomerates. But while these sandstones and conglomerates usually are red or reddish and only rarely grey in the Wood Bay series, they are, on the contrary, generally green or grey-green in the Red Bay series, though in certain places — as for instance, at the Fränkel Ridge and the uppermost parts of Mt. Pteraspis — they may even in the latter series have a grey or red colour. The skeletal parts which occur in the red or grey rocks are generally whitish, pink or reddish in colour, often with a tone of blue in it when they have been exposed to weathering. On the other hand, the skeletal parts which are embedded in the green or grey-green rocks are in an unweathered condition dark-brown or black owing to infiltration by bitumen. When exposed to weathering, they often loose the bitumen and change their colour into reddish-blue, light blue or almost white.

The cephalic shields from the Wood Bay series usually have the internal parts more or less destroyed and crushed or are in most cases so badly preserved that few details can be observed. The cephalic shields from the Red bay series, especially several of those of small species, on the contrary, often have their internal parts in an excellent state of preservation; and as in addition their bone, by its dark colour, strongly contrasts with the comparatively light rock, they are very well suited for a detailed study of the internal anatomy.

In order to get an idea as comprehensive as possible of the internal structures certain of the shields from the Red bay series were prepared by hand so that the different canals etc. became exposed, while other specimens from this series were used for serial sections.

Since the details to be prepared by hand were in most cases extremely delicate the preparations had to be made by very fine needles under a binocular loupe of a modern construction, as manufactured by Zeiss. The magnification generally used for this purpose was about 30—50 times. In order to eliminate the refractions caused by the rather coarse grains of the rock — that is to say in order to intensify the contrast in colours between the often extraordinarly thin and not very distinct bone laminae and the rock — most of these preparations had to be carried out in alcohol or diluted Canada balsam. As the rock was usually very hard the preparations required a considerable time. It may be mentioned, for instance, that the preparation of the specimen shown in pls. 49 and 50 took about two months.

The serial sections were made by grinding, according to the method invented by SOLLAS (1904 b). As the material which could be used for this purpose, however, was very limited and as in addition it was in the first place necessary to establish the course and relations of several of the very fine canals the sections in some of the series, as for instance in the transverse series B and the sagittal series C, have not been taken with quite regular intervals. Each section was drawn by a Zeiss drawing camera. And in order to make the details as distinct as possible for the drawing the ground surface was covered with thin canada balsam, glycerine or eugenol. Or else in certain cases it appeared for the same purpose more favorable to submerge the entire piece of rock with the fossil into one of the said fluids. The section series A, B, D, and F figured in pls. 74—114 are so complete that they could be used for making models in wax of the fossils and the restorations given in text-figs. 14—27, 33—35, and 39—41 are reproductions of certain of the models thus made.

Anatomy.

General characters.

Shape and mode of living. — As has been pointed out already by several previous writers, the Cephalaspids, with regard to their general shape, rather closely resemble certain recent Loricarioid Teleosts, a state of things which, as is now well known, is due to convergence. Their head is always broad and more or less depressed in a dorsi-ventral direction with the eyes situated close together on the dorsal side and the mouth and the branchical openings on the ventral side.

From their general shape it is easily understood that the Cephalaspids were benthonic forms. And since, as we shall see from the description given below, they had no jaws their mode of feeding must have been rather passive. Probably, therefore, their food consisted either of small invertebrates living on and in the mud or of these together with putrefied organic substances.

The cephalic shield, its subdivision and certain of its external characters. — The head and an adjacent more or less long part of the trunk are provided with a continuous shield which, in the fossil state, consists only of bone. This shield has usually been called the cephalic shield, a term which will be adopted for it throughout this work too. The part of the cephalic shield as thus defined that belongs to the head, and which will be termed the cephalic division proper, is from the outside not distinctly bounded off from the other part which falls in the most anterior part of the trunk and which will be referred to as the trunk or abdominal division. The approximate extension of these two divisions is shown in text-fig. 1.

The cephalic division proper completely occupies the parts of the head visible from the dorsal side. On the ventral side of the head, on the contrary, it is restricted to a marginal zone along the rostral and lateral borders and to a posterior zone which connects the posterior part of the marginal zone of one side with the posterior part of the marginal zone on the other side (text-fig. 1 B)[1]. Accordingly it forms on the ventral side a more or less distinctly ring-like zone which posteriorly is continuous with the trunk division of the shield. This zone will in its entirety be referred to as the ventral rim, and this term is thus used here in a wider sense than in the earlier works, and as proposed by LANKESTER (1870) and WOODWARD (1891 a).

Owing to the fact that it thus does not occupy anything like the whole of the median parts of the ventral side of the head, the cephalic division proper has in the fossil state of preservation a big opening ventrally, an opening which is bounded anteriorly and laterally and posteriorly by the medial margin of the ventral rim. This opening leads upwards into a large space which lodged the pharynx, the gill-sacs and the mouth, and which may therefore be properly called the oralo-branchial chamber (text-figs. 2, 4). The opening itself, which has an oval or more or less circular shape (text-fig. 1 B, 4, 8 B), may be termed the oralo-branchial fenestra.

The oralo-branchial fenestra was in the living specimens closed by soft tissue which was perforated by the mouth opening anteriorly and by the external openings of the gill-sacs along each lateral side just as in *Tremataspis* (PATTEN 1903 a, Pl. 2). This soft tissue certainly contained one or several skeletal elements of cartilage; and, at least in several forms, the external (ventral) side of it was protected by an armour consisting of numerous small, closely set scales or plates of

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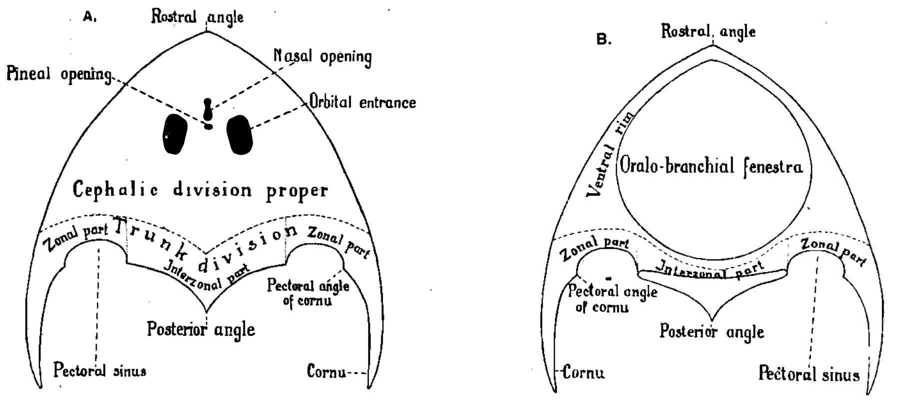
[1] In certain of the English forms — as for instance *Hemicyclaspis murchisoni* — the posterior zone as well as the ventral part of the trunk division are represented merely by scales.



Text-fig. 1. Sketch of the cephalic shield of a *Cephalaspis*. The approximate boundaries between the different divisions denoted by broken lines.

various shape and size. This was the case, for instance, in *Hemicyclaspis murchisoni* (WOODWARD 1891 a, p. 189, pl. X, fig. 2) and in *Cephalaspis straxrudi*, the latter of which is from the Spitsbergen Downtonian[1]. In this connection it deserves also to be pointed out that the corresponding part of the ventral side of the head in *Tremataspis* was provided with a number of plates of a similar kind (PATTEN 1903 a, pp. 7—12, pl. 2), although these plates were larger and fewer than those known so far among Cephalaspids.

As is seen from text-figs. 2, 3, 5 the cephalic division proper is low both anteriorly and along the lateral borders. The rostral margin is in dorsal and ventral aspcects in certain forms rather rounded off (text-figs. 61, 63, 76; pl. 3, fig. 2, pls. 6—8, 42; pl. 43, fig. 1), whereas in others it is provided with a more or less pronounced angle — the rostral angle (text-figs. 1, 53, 65, 66 etc.; pl. 1, fig. 1; pl. 5, fig. 1; pl. 23, fig. 1; pl. 32, fig. 1; pl. 36, fig. 2 etc.). In certain forms, as *Cephalaspis campbeltonensis* (WOODWARD 1891 a, p. 191, pl. 9, fig. 5; TRAQUAIR 1893 a, pp. 146—147), *Boreaspis rostrata* (text-figs. 78; pl. 13, fig. 4; pls. 14, 15) and *Hoelaspis angulata* (text-fig. 77; Pls. 44, 45), it may even be produced into a more or less long rostral process.

On the dorsal side of the cephalic division proper we find the following structures: the orbital openings, the unpaired nasal opening, the unpaired pineal opening and an unpaired and a paired field which, owing to their supposed function, will be referred to as the electric fields.

The orbital openings, which in most forms are rather large, are as a rule oval in shape, with their longest axes approximately parallel to the longitudinal axis of the head, or slightly converging forwards or

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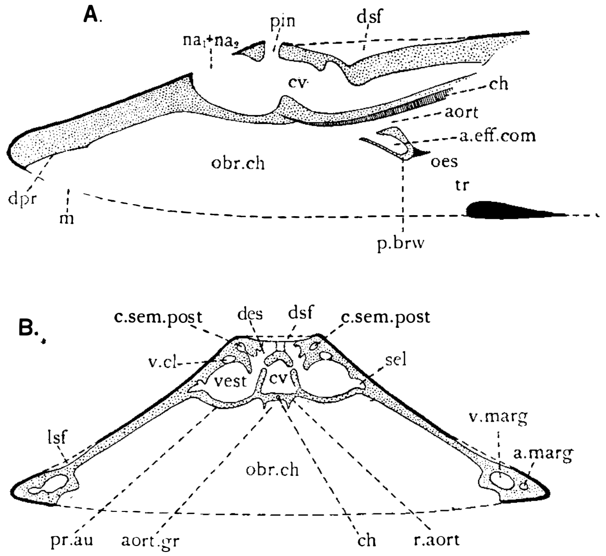
[1] In *Hemicyclaspis murchisoni* these plates or scales were continued backwards by the scales of the ventral side of the trunk.

backwards. They face not only dorsally but also laterally, more laterally, however, in those forms which have a high cephalic shield than in those which have a low cephalic shield (text-figs. 3, 5—8, 53—79; several plates). In most forms they are surrounded externally by a somewhat raised, thickened border which has been called the orbital ring by LANKESTER (1870, p. 37) and the orbital rim by WOODWARD (1891 a, p. 178).

The nasal opening, which — as already pointed — out is unpaired, lies in the median line close in front of the pineal opening with a posterior part generally reaching somewhat backwards between the orbital openings. It is extended in the longitudinal direction of the head so that it is much longer than broad. At least in all forms known at all fully it consists of three divisions, an anterior one (na_1) and a posterior one (na_2), which are rather circular or oval, and a middle narrow one, which is more or less slit-like and connects the two other ones (text-figs. 1, 3, 7, 8, 15, 20, 23, 27; pl. 6, fig. 2; pls. 8, 17; pl. 32, fig. 2; pl. 35, figs. 1, 2; pl. 36, fig. 1; pls. 39, 41; pl. 43, figs. 2, 4; pl. 46, fig. 2). As far as is known, it is always situated in a distinct depression (*f. cn*, text-fig. 3; pl. 17; pl. 32, fig. 2) which was called by LANKESTER (1870, p. 37) the antorbital fossae (cf. also WOODWARD 1891 a, p. 178), but which more conveniently may be termed the fossa circumnasalis, a name which will be employed for it throughout this paper. In *Thyestes verrucosus* (PATTEN 1903 c, fig. 9, p. 846; JAEKEL 1911, text-fig. 20), and perhaps in other forms too, the nasal opening seems to be situated at the very bottom of the fossa circumnasalis. In most of the Spitsbergen forms (*C. hoeli* and others), on the contrary, the nassal opening lies on a slight though distinct longitudinal elevation which rises from the bottom of the fossa circumnasalis (text-fig. 3; pl. 17; pl. 32, fig. 2). The functions of the different parts of the nasal opening will be dealt with in connection with the description of the cranial cavity.

The pineal foramen (*pin*, text-figs. 1 A, 3, 7, 8 A, 15, 20, 23, 27, 53—79; pl. 6, fig. 2; pl. 8; pl. 13, figs. 2—4; pl. 17; pl. 35, figs. 1, 2; pl. 36, figs. 1, 2; pl. 38, fig. 1; pls. 39—41; pl. 43, fig. 1; pl. 46, fig. 2) lies between the orbital openings — as a rule between the middle parts of these — and is sometimes broader than it is long, sometimes slightly longer than it is broad and finally sometimes almost circular. The material which I have studied however, does not give any certain evidence as to whether its shape is constant to each species or wheter it varies so much that it may have a different shape in different specimens of the same species. In certain forms e. g. *Ateleaspis* (text-fig. 6; TRAQUAIR, 1905, fig. 3, on p. 884), *Hemicyclaspis* (*Cephalaspis*) *murchisoni* (WOODWARD 1891 a, pl. X, fig. 1; PATTEN 1903 c, pl. 1, figs. 1—4) and a few others (pl. 43, fig. 4) the pineal foramen was probably situated in an independent narrow transversal plate of bone which extended between the two orbital openings in the manner shown in text-fig. 6.



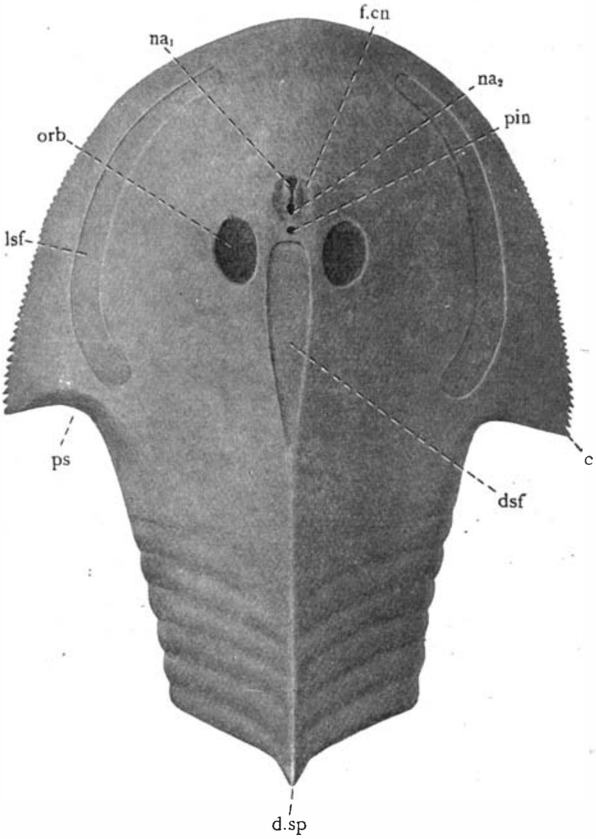
Text-fig. 2. Two schematic sections through the head of a Cephalaspid. *A*, median sagittal section. *B*, transverse section through the posterior part of the otic region. The exoskeletal bone with thick lines and the perichondral bone-layers with fine lines; cartilage dotted.

a. eff. com, space for the arteria branchialis efferens communis; *aort*, aorta canal; *aort, gr.* aortal groove, *a. marg*, canal for the marginal artery; *ch*, notochord; *c. sem. post*, division of the labyrinth cavity for the canalis semicircularis posterior; *cv*, cranial cavity; *dpr*, area which bounded the mouth cavity on the dorsal side; *des*, canal for the electric nerve to the dorsal electric field; *dsf*, dorsal electric field; *lsf*, lateral electric field; *m*, mouth opening; $na_1 + na_2$, nasal opening + the opening of the hypophyseal sac; *obr. ch*, oralo-branchial chamber; *oes + tr*, opening for the oesophagus and the truncus arteriosus in the postbranchial wall; *p. brw*, post-branchial wall; *pin*, pineal foramen; *pr. au*, otical prominence; *r. aort*, aortal ridge; *sel*, one of the nerve-canals to the lateral electric field; *v. cl*, canal for the vena capitis lateralis; *v. marg*, canal for the marginal vein; *vest*, vestibular division of the labyrinth cavity.

The structures referred to above as electric fields are depressed distinctly bounded areas which in certain well-preserved specimens of *Cephalaspis*, *Hemicyclaspis murchisoni*, *Aceraspis* and *Tremataspis* are covered by numerous small polygonal plates (Woodward 1891 a, pl. X, fig. 2; 1906, fig. 2; 1920 fig. 4, p. 32; Patten 1903 c, text-figs. 5, 6, 9, pl. 1. fig. 3; 1912, figs. 232, 238; Goodrich 1909, fig. 173; Jaekel 1911, figs. 20, 21; Stromer 1912, fig. 50; Kiaer 1924, text-fig. 10). In the Spitsbergen forms, however, nothings is preserved of such plates. The unpaired electric field lies immediately behind the pineal opening, extending from that more or less far backwards. This field will be called here the dorsal electric field (*dsf*, text-figs. 2 A, 3, 53, 56, 57, 64, 65, 67, 74, 76—79; pl. 1, figs. 2, 3; pl. 3, figs. 2, 3; pl. 13, fig. 4; pl. 17; pl. 19, fig. 2; pl. 32, figs. 1, 2; pl. 38, fig. 1; pl. 39; pl. 46, fig. 2). The paired electric field, which is situated rather close to the lateral margin of each side, is always rather long; and in those species which have broad cornua it extends regularly backwards on these, in certain species even almost to their distal ends. Throughout this work the paired electric field will be referred to as the lateral electric field (*lsf*, text-figs. 2 B, 3, 5, 53, 56, 57, 58, 61, 64, 65, 67, 68, 71, 74, 75—79; pls. 1—3; pl. 4, figs. 1, 2; pl. 8; pls. 11, 14, 20—22; pl. 23, fig. 2; pls. 28—30; pl. 31, fig. 3; pl. 32, figs. 1, 2; pl. 38, fig. 1, pls. 45, 49, 50; pl. 54, fig. 1). While in most Cephalaspids the lateral electric field throughout its length generally is a continuous organ, there is known a form, *Eukeraspis*, in which, according to the accounts by LANKESTER (1870, text-fig. 31, p. 58) and WOODWARD (1891 a, text-fig. 27, p. 193) it is subdivided into six different divisions. In this connection it is also worthy of notice that the lateral electric field in *Tremataspis* is subdivided too though the divisions are only two, an anterior and a posterior one, which lie far apart (PATTEN 1903 a, pp. 23—26, pl. 2, fig. 9; 1912, figs. 236, 238; JAEKEL 1903, pp. 86—89, fig. 1; 1911, p. 34, fig. 19; WIMAN 1918). The minute structure, innervation and function of the electric fields will be dealt with in a special chapter below.

The trunk division of the cephalic shield is composed of one median unpaired part and a paired lateral part (text-fig. 1), the latter of which includes also the cornu of its side. The pelvic fin articulated against this latter part which thus corresponds to a shoulder girdle, and on account of that it is referred to in the present work as the zonal part (text-fig. 1). The unpaired part which protected the portion of the trunk situated medially and posterior to the zonal part of each side will be called the interzonal part (text-fig. 1).

The interzonal part, as thus defined, is continuous with the cephalic division proper anteriorly and with the zonal part at each antero-lateral corner (text-fig. 1). In most forms it exhibits no or only very indistinct traces of segmentation. On the otter hand in a few forms such as *Hemicyclaspis murchisoni* (WOODWARD 1891 a, pl. X, fig. 1; JAEKEL 1911, fig. 21), *Cephalaspis lyelli* (GOODRICH 1909, text-fig. 173; STROMER 1912, fig. 50), *Thyestes verrucosus* (ROHON 1896 a, text-fig. 4; PATTEN 1903 c, text-fig. 9; JAEKEL 1911, fig. 20) and *Kiaeraspis auchenaspidoides* (text-fig. 3—5, 79; pl. 52; pl. 53, fig. 1; pl. 54, fig. 2, pl. 55) there are to be seen on the posterior parts of its lateral surface several dorsiventrally running grooves separated by ridges, which have approximately the same breadth as the high flank scales of the trunk and obviously must represent such flank scales which thus have been incorporated in the cephalic shield. In *Kiaeraspis* there are in addition on the ventral surface (pl. 53, fig. 2) most posteriorly quite distinct traces of small more or less quadrangular scales, so that it is there fully obvious that the ventral portion of the interzonal part has arisen by fusion of small independent ventral scales. Under the supposition that on the trunk the high flank-scales corresponded in number to the myomeres there would thus be a possibility to ascertain the number of segments forming the interzonal part of the cephalic shield. Since, however, the boundaries between the originally independent scales in the anterior portion of the interzonal part are either very indistinct (*Thyestes verrucosus*) or have entirely disapeared, only an approximate estimation of the number of



Text-fig. 3. *Kiaeraspis auchenaspidoides.* Restoration of cephalic shield. Dorsal view. $^{4,5}/_1$. *c*, cornu; *dsf*, dorsal electric field; *d. sp*, dorsal spine; *f. cn*, fossa circumnasalis; *lsf*, lateral electric field; *na*$_1$, opening of the hypophyseal sac.; *na*$_2$, nasal opening proper; *orb*, orbital opening; *ps*, pectoral sinus; *pin*, pineal foramen.

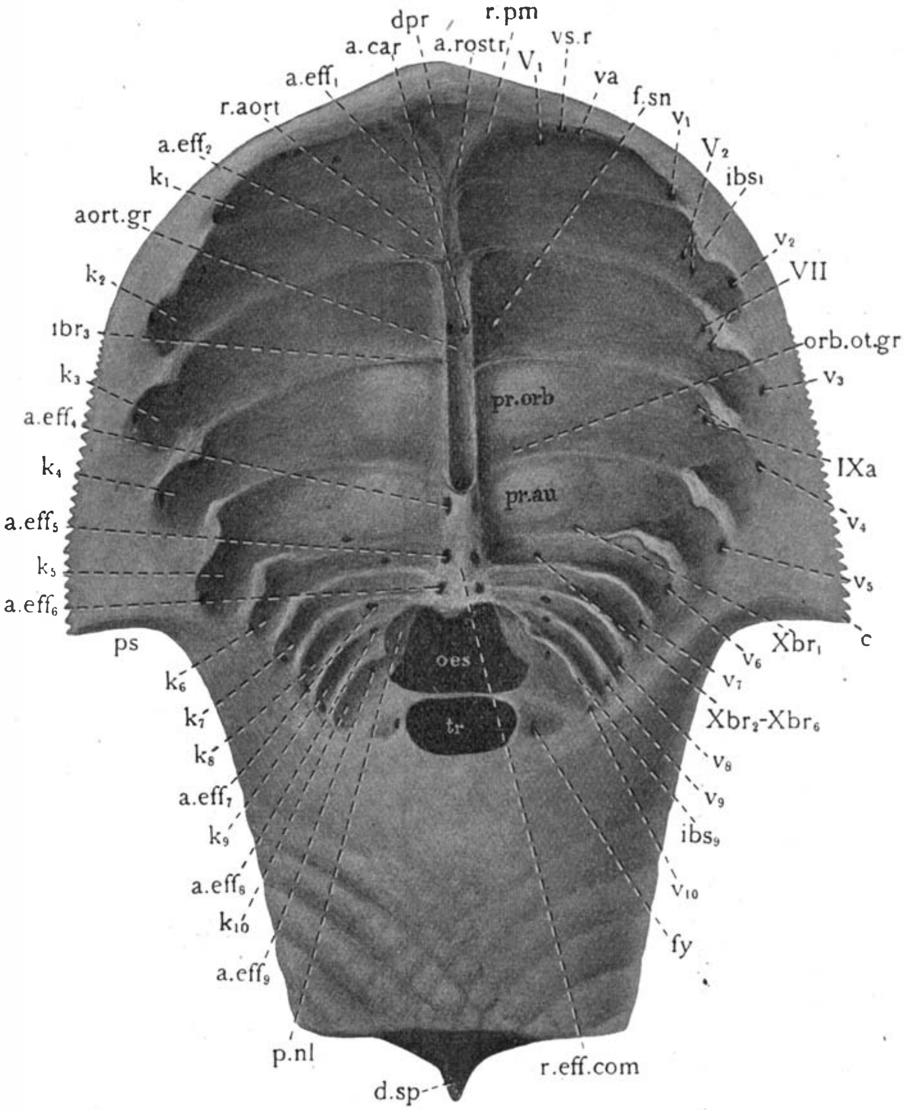
segments can be made. Such an estamation gives as a result that the number of segments would be in the *Cephalaspis*-species generally 2—3, in *Thyestes verrucosus* 4 or 5 and in *Kiaeraspis auchenaspidoides* 9—10. At least in several *Cephalaspis* species (*C. hoeli* and others) and in *Kiaeraspis auchenaspidoides,* it is fully obvious that the interzonal part is one segment shorter ventrally than laterally and dorsally (text-figs. 3—5, 79; pl. 53, fig. 2). As is thus seen from what has been seth forth here, the interzonal part varies rather much in extension backwards according to the number of segments of which it consits.

The dorsal side of the interzonal part is in several forms somewhat extended backwards, forming a more or less pronounced angle, which is here termed the posterior angle of the cephalic shield (text-fig. 1). In certain forms, as *Cephalaspis lyelli* (LANKESTER 1870, text-fig. 16), *Cephalaspis isachseni* (text-fig. 57; pl. 3), *Cephalaspis hoeli* (text-fig. 64; pl. 19, fig. 3), *Kiaeraspis auchenaspidoides* (text-fig. 3, 5, 79; pl. 54, fig. 1; pl. 56, fig. 2) and others, this angle is elevated and developed into a dorsal spine, which as has been suggested by KIAER (1911, p. 16) probably forms the last vestige of the reduced anterior dorsal fin. In several forms a more or less sharp median longitudinal ridge or keel, the crista longitudinalis dorsalis, extends from the posterior angle or the dorsal spine forwards to the posterior end of the dorsal electric field. In other forms such a ridge or keel is indistinctly developed or absent. The angle between the posterior and lateral borders of the interzonal part was called by LANKESTER (1870, p. 38) the posterior angle of the shield; but as, save in a few exceptional cases (*Benneviaspis holtedahli*, text-fig. 76; pl. 43, fig. 1), it actually does not reach as far back as the angle termed here the posterior angle, it will be called instead the postero-lateral angle (text-fig. 1).

Turning now to the zonal part, we find (text-fig. 1) that this, without any boundaries, is continuous anteriorly with the cephalic division proper of the shield. As will be shown later it has a posterior wall perforated by several canals, and against this wall the pectoral fin articulated (text-figs. 34, 35, 52; pl. 54, fig. 1). Concerning this fin it is further to be mentioned that it was situated with its anterior portion in the sinus, which, as a rule, is formed by the posterior margin of the zonal part. This sinus, which therefore will be called the pectoral sinus (text-fig. 1; *ps*, text-figs. 3, 4, 5 and most of the plates), is bounded laterally by the cornu of its side and medially by the interzonal part of the shield. In certain forms the cornu has on its medial side an obtuse angle, which indicates how far the pectoral sinus reaches backwards on the lateral side. This angle will be referred to as the medial angle of the cornu (text-fig. 1; pl. 2, fig. 3; pl. 2, figs. 3, 4; pl. 4, fig. 1; pl. 11).

The pectoral sinus, as here defined, is generally well developed and distinctly bounded in the *Cephalaspis*-species and further it is also well developed in *Eukeraspis*. In *Hemicyclaspis murchisoni* and in *Hoelaspis* it is broad and not distinctly bounded; and probably this was the case in *Aceraspis* and *Micraspis* too (KIAER 1911, pp. 16—17; 1924, text-fig. 10). In *Thyestes*, *Boreaspis* and *Kiaeraspis* it is rather small which probably indicates that the pectoral fin was somewaht reduced in these genera. In *Didymaspis* I have found it too, though it is very small (text-fig. 80; cf. WOODWARD 1891 a, pl. IX, figs. 7, 8). In *Tremataspis*, on the contrary, no traces of it can be detected. Its gradual disappearance in *Thyestes* — *Boreaspis* — *Kiaeraspis* — *Didymaspis*, however, seems to indicate that its absence in *Tremataspis* is due to reduction. A further support for such a view is formed, as we shall see, by the fact that also other groups among the Ostracoderms than the Cephalaspids have traces of pectoral fins.

In *Ateleaspis* the postero-lateral "lappet-like expansions" of the cephalic shield were considered by TRAQUAIR (1899 c, p. 858; 1904,



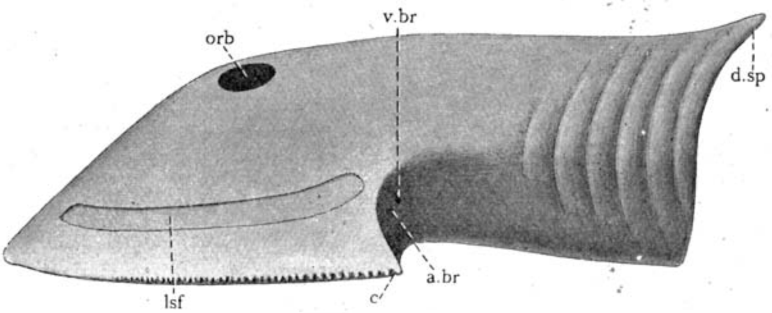
Text-fig. 4. *Kiaeraspis auchenaspidoides.* Restoration of cephalic shield in ventral view. 6/1. *a. car,* carotid canal; *a. eff*$_1$,—*a. eff*$_2$, grooves for the two most anterior efferent branchial arteries; *a. eff*$_4$—*a. eff*$_9$, canals for the efferent branchial arteries 4—9; *aort. gr,* groove for the aorta; *a. rostr,* groove for the rostral artery (the premandibular efferent branchial artery); *c,* cornu; *dpr,* excavated or depressed area, which formed the roof of the mouth; *d. sp,* dorsal spine; *f. sn,* subnasal fossa; *fy,* canal probably for a ventral longitudinal superficial vein; *ibr*$_3$ interbranchial ridge 3; *ibs*$_1$, *ibs*$_9$ interbranchial septa 1 and 9; *k*$_1$—*k*$_{10}$, branchial fossae; *oes,* opening through the postbranchial wall for the oesophagus; *orb. ot. gr,* orbito-otical groove; *p. nl,* pronephros lamella; *pr. au,* otic prominence; *pr. orb,* orbital prominence; *ps,* pectoral sinus; *r. aort,* aortal ridge; *r. eff. com,* ridge that lodged the arteria branchialis efferens communis; *r. pm,* prebranchial ridge; *tr,* foramin through the post-branchial wall for the truncus arteriosus; *v*$_1$—*v*$_{10}$ canals for ventral transversal superfical veins; *va,* canal probably for a branch of the truncus arteriosus that posteriorly anastomozed with the marginal artery and marginal vein; *vs. r,* rostral vein sinus; *V*$_1$, canal for the n. profundus; *V*$_2$, canal for the n. trigeminus proper; *VII,* canal for the n. facialis; *IX a,* canal for the n. glossopharyngeus; X$_{\mathrm{br}1}$, canal for the first branch of the n. vagus; X$_{\mathrm{br}2}$—X$_{\mathrm{br}6}$, canals for the other branchial barnches of the vagus nerve.

pp. 885—886) to be homologous with the "flap-like structures in *Chephalaspis*", i. e with the structures called in this work the pectoral fins. It seems not improbable, however, that the "lappet-like expansions" in *Ateleaspis* (text-fig. 6) — if they really were as in the restoration given by TRAQUAIR — instead represent the cornua and perhaps certain proximal parts of the pectoral fins, and that both are in a much reduced state. Another possibility, which also is to be taken into account, is that the "lappet-like expansious" are only the cornua and that the pectoral fins were in a much reduced state and devoid of scales so that nothing therefore could be left of them in the fossils. In any case, from what has been said above concerning the presence of pectoral fins in Cephalaspids and other Ostracoderms it seems highly probable that the peculiar appearance of the postero-lateral parts of the cephalic shield in *Ateleaspis* are due to reductions and transformations of conditions rather like those in *Cephalaspis.* This is the more probable since *Ateleaspis* in most other respects obviously is a typical Cephalaspid.

Finally also the cornua ought to be taken into consideration in this connection. These structures always form parts of the cephalic shield, and, as has been pointed out, they are probably simply the enlarged and produced postero-lateral corners of the zonal part of the trunk division of the cephalic shield. In other words: they thus presumably belong to the shoulder-girdle, constituting lateral parts of that. In *Hoelaspis* they point almost straight laterally, in other forms generally more or less postero-laterally or posteriorly. With regard to their shape they may be either broad and rather flat in a dorsi-ventral direction (text-figs. 54—56, 58, 60, 61; pls. 1, 2, 11) or else narrow and more or less circular in transverse section (text-figs. 57, 70, 71; pl. 3). Their medial border is in certain species provided with denticles. The cornua are generally well developed in the *Cephalaspis*-species as well as in *Benneviaspis* and *Hoelaspis* (text-figs. 76; 77; pls. 42—47). In *Kiaeraspis*, *Boreaspis* and *Thyestes* they are smaller but nevertheless very distinct. In *Hemicyclaspis murchisoni*, *Ateleaspis*, *Aceraspis*, *Micraspis* they are very slightly developed. In *Didymaspis* they are even so small that they have hitherto generally been overlooked and finally in *Tremataspis* they are, as is well known, entirely absent.

The dermal and primordial components of the cephalic shield. — The cephalic shield consists both of a dermal component, which will be referred to as the exoskeleton, and of a primordial component for which the term endoskeleton, will be employed. The endoskeleton has hitherto been overlooked owing to the circumstance that detailed investigations of the interior parts of the cephalic shield can be carried out only in exceptional cases.

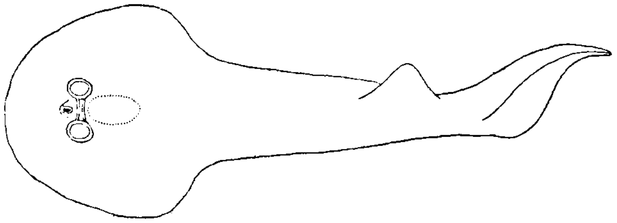
The exoskeleton has a superficial position as usual, but it was certainly very closely connected with the endoskeleton in those places



Text-fig. 5. *Kiaeraspis auchenaspidoides.* Restoration of cephalic shield. $^{4,5}/_{1}$. *a. br,* foramen for the arteria brachialis; *c,* cornu; *d. sp,* dorsal spine; *lsf,* lateral electric field; *orb,* orbital opening; *v. br,* foramen for the vena brachialis.

at which this was present basally to it. It alone forms the ventral and lateral walls and to a considerable extent also the dorsal wall of the interzonal part of the cephalic shield, whereas otherwise it was developed in relation to the endoskeleton. It is generally thick and strong, but may in certain forms — as *Ateleaspis* and also in several *Cephalaspis*-species from the Spitsbergen Devonian — be rather thin. Further details of its structure will be given below in the account on the minute structure of the bone of the cephalic shield.

The endoskeleton is situated on the inside of the exoskeleton and extends as far antero-ventrally and latero-ventrally as that. On the contrary, it reaches less far backwards, as is seen from text-figs. 7, 8, 9—12, (cf. also pl. 23, fig. 3), so that the interzonal part, as has been pointed out, is chiefly formed by the exoskeleton alone. As is also shown by the text-figures quoted, the endoskeleton is throughout its extension a continuous structure. Since in its dorso-median part it lodged the brain, the auditory organs, the eyes, the olfactory organ and the cephalic portion of the notochord (text-fig. 2; pl. 49) it is quite clear that it comprised the whole primordial neurocranium or, as it will be termed here, the endocranium. Moreover, as with its anterior, lateral and posterior parts, it extends downwards to the external branchial openings (text-figs. 2, 8 B, C, 37, 79; pls. 15, 51), and, as we shall see, it has on the side exposed in the oralo-branchial chamber very distinct impressions which were related to the branchial apparatus, there can be no doubt that it also includes homologues of the dorsal parts of the visceral arches and thus at least partly the visceral endoskeleton. Further as with its most posterior part it reaches backwards into the cornua and to the pectoral sinus, forming there the articulation surface for the pectoral fin it obviously comprises the endoskeletal shoulder-girdle too (text-figs. 7, 8; *p. sh,* text-figs. 9—12, 52; pl. 10; pl. 54, fig. 2). Finally there is found in it a part which probably formed a protection for the pronephros (*p.nl,* text-figs. 9, 10, 34, 35).



Text-fig. 6. *Ateleàspis tesselata.* Diagrammatic restored outline after TRAQUAIR 1904.

It is thus seen that the endoskeleton of the cephalic shield is a very complex structure.

In *Boreaspis rostrata* from the very lowest Devonian of Spitsbergen the endoskeleton is almost throughout well ossified, consisting of cancellous bone, which on the surfaces, which are freely exposed in the fossil, as well as in all cavities and canals is lined with thin layers of perichondral bone which are continuous with the basal layer of the exoskeleton and pass over into that. The cancellous interior, when seen in section, appears as a network (pls. 14, 15) and is somewhat suggestive of the middle layer of the shield in the Pteraspids.

In all the Silurian (Downtonian) forms which I have had the opportunity of studying the endoskeleton was completely ossified only in the posterior parts of the cornua. Otherwise it must have consisted of an uncalcified solid tissue, which cannot have been anything else but a sort of cartilage, perhaps, as we shall see, a cartilage nearest comparable to the mucous cartilage found in the larvae of the Petromyzontids. This cartilage was, as a rule, lined with perichondral bone-layers on the surfaces not covered by the exoskeleton and on the surfaces of all cavities and canals. These perichondral bone-layers are continuous both with each other and with the exoskeleton.

The different layers of perichondral bone which are found in the Silurian forms — at least in those from the Spitsbergen Downtonian — are as follows: 1) the internal layer, 2) the labyrinth layer, 3) the orbital layer, 4) the external layer and 5) the canal layers. More closely defined these layers have the following extensions and relations.[1]

1) The internal layer forms a continuous covering of the entire cavum cerebrale cranii.

2) The labyrinth layer forms a continuous lining of the entire labyrinth cavity (cavities for the semicircular canals included). By means of canal layers it is continuous with the external and internal layers, with the orbital layer and with the exoskeleton.

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[1] All these layers are, of course, also present in *Boreaspis rostrata.*

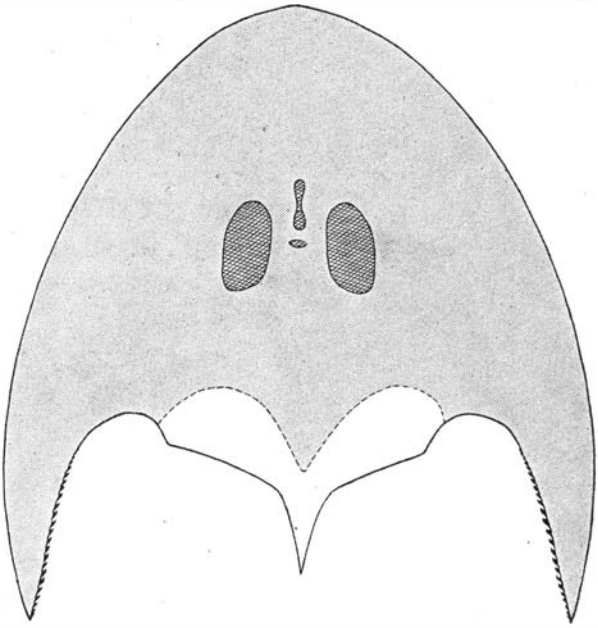
3) The orbital layer forms a continuous lining of the orbit. It is continuous directly with the internal layer and with the exoskeleton. In addition certain canal layers connect it with the external and internal layers as well as with the labyrinth layer.

4) The external layer is found on the external surfaces of the endoskeleton, which are not covered by the exoskeleton. Thus it lines the oralo-branchial chamber, the posterior surface of the wall — the postbranchial wall — which bounds this chamber posteriorly (*p. brw*, text-figs. 2 A, 4) and the ventral side of those parts of the endocranium that, as we shall see, project backwards beyond the postbranchial wall. Finally it is also present on the posterior surface of each zonal part of the shield, where it forms the articulation-surface for the pectoral fin. It thus forms a lining membrane also on the posterior surface of the endoskeletal shoulder-girdle. It is continuous directly with the exoskeleton, and by means of canal layers, with the internal and external perichondral bone-layers. A lateral portion of this bone-layer has been observed by HUXLEY (1858 a, p. 271; pl. 14, fig. 4) and LANKESTER (1870, p. 36, text-fig. 13).

5) The canal-layers line the canals for vessels and nerves that traverse the endoskeleton, and they are generally present even in very narrow canals. As has already been emphasized in dealing with the other perichondral layers, these, even when they do not pass directly over into each other, are nevertheless continuous with each other by a number of canal-layers. The canal layers which line canals to the exoskeleton are at the distal ends of these canals continuous there with that, more exactly with the basal layer of it.

As is evident from the facts now brought forward, the various perichondral bone-layers form, by means of their connections with each other, a large continuous bone which in its turn is continuous with the exoskeleton. The cephalic shield of the Silurian Cephalaspids is thus a single large bone which was cartilaginous in the interior of its endoskeletal component.

Finally in the Devonian Cephalaspids, with the exception of *Boreaspis rostrata* already treated, the conditions whith regard to the degree of ossification of the endoskeleton seem to be chiefly as in the Silurian ones (pls. 7—10). It is noticeable, however, that in them the perichondral bone-layers may often be entirely absent, and that even in well preserved specimens such as — for instance the specimen of *Cephalaspis isachseni* figured in pl. 3 — they are much less complete than in the Silurian forms. These conditions cannot, in my opinion, have been caused merely by unfavorable conditions during the process of fossilization, but must in addition be owing to some other cause. And as far as I can understand at present, that cause is probably to be sought for in a less strong development of the perichondral bone-layers

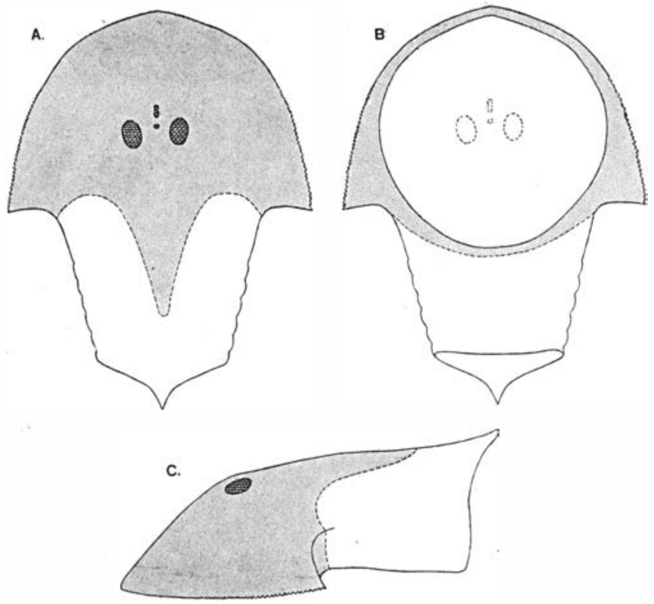


Text-fig. 7. *Cephalaspis hoeli.* Sketch showing the approximate extension of the primordial component of the cephalic shield. The primordial component shaded.

themselves. To put the matter in another way, the perichondral bone-layers in most Devonian forms were conceivably in a more or less reduced state so that generally they could not be well preserved.

From what has been set forth here, it thus seems as if the perichondral layers were better developed in the forms from the Silurian and the very lowest Devonian than in the forms from the somewhat younger deposits of the lower Devonian. And, as will be shown in the account below, the exoskeleton seems also to be thicker and stronger in the majority of the Downtonian forms than in the forms from the lower Devonian. There are thus certain facts which seem to point to the view that the Cephalaspids, like the *Arthrodires* (Stensiö, 1925 b), the *Dipnoi* (Stensiö, 1925 b, p. 162), the *Coelacanthidae* (Stensiö 1922; 1923) and the majority of *Chondrostei* (Stensiö, 1921; 1925 a; Watson 1925), represent a degenerating series with regard to their degree of ossification.

Minute structure of the bone of the cephalic shield.— Contrary to what might be expected from its macroscopic appearance, the bone tissue of the cephalic shield is, as a rule, in all Spitsbergen forms badly preserved with regard to the microscopic structure. Hence my researches into its finer details could not be carried out with the completeness which would have been desirable, and accordingly the account given here can by no means claim to be exhaustive.



Text-fig. 8. *Kiaeraspis auchenaspidoides.* Sketch to show the approximate extension of the primordial component of the cephalic shield. The primordial component shaded. *A* in dorsal, *B* in ventral and *C* in lateral view.

We begin with the exoskeleton. But before dealing with the minute structure of that, we must first consider certain of its macroscopic features.

The exoskeleton is generally thickest in those parts which cover the ventral rim, the cornua and the anterior and lateral margins of the endoskeleton (pl. 63; pl. 66, fig. 2; pl. 67, fig. 2). Further it is rather thick around the orbit. It is thinnest on the dorsal side of the endoskeleton in front of the nasal opening and dorso-medially to each lateral electric field, between that on the one hand and the orbital opening and the dorsal electric field on the other (pls. 8, 9, 10).

The external surface of the exoskeleton is in most forms subdivided by grooves — the interareal grooves (*iag*, pl. 64, fig. 2; pl. 71, fig. 1) — into the well-known polygonal areas (pl. 8; pl. 16, fig. 2; pl. 43, fig. 4; pl. 71, fig. 1) or tesserae. The fact may, however, be emphasized here that in several of the small forms — such as *Cephalaspis hoeli*, *Cephalaspis vogti*, *Benneviaspis*, *Hoelaspis* and *Kiaeraspis* — I have not been able to observe any subdivision into polygonal areas. On the inner (basal) surface of the exoskeleton there are mostly no distinct traces of these areas, but in certain forms with very thin exoskeleton the interareal grooves give rise to ridges on the inner surface of the exoskeleton by their depressed bottoms. We thus have in these forms the polygonal subdivision of the outer parts of the exoskeleton reflected on the inner side, although the interareal grooves are there represented by ridges and the polygonal areas by depressions (pl. 8).

Beneath the exoskeleton, and partly enclosed in the most basal part of the basal layer of it there are on the outside of the endoskeleton a great number of superficial vascular canals, which branch abundantly, forming with their branches a fine network or plexus, the subaponeurotic vascular plexus, which will be described in detail in another place below. This plexus is well shown from above and below in plates 25, 39, 45, 49, 50, and in section (*dplx*) in pl. 64, fig. 2; pl. 65; pl. 66, fig. 2. It is not impossible that, at least so far as the Spitsbergen material is concerned, this plexus in certain of the Downtonian forms is more completely enclosed in the exoskeleton than it is in the Devonian forms. If it could be shown that this difference is not due to an occasion, and in addition that it was not a mere exception in a few forms, it would of course mean that the basal layer of the exoskeleton was less developed basally in the Devonian forms than in the Downtonian ones, or to put it in another way: these conditions would indicate that the deepest part of the exoskeleton of the Devonian forms often had become reduced to a certain extent, as compared with that of the Devonian ones.

From the subaponeurotic vascular plexus numerous fine branches are given off to the exoskeleton. These branches (*c.asc*, pl. 63; pl. 64, fig. 2; pl. 65, fig. 2; pl. 67, fig. 1; pls. 69, 70), which will here be called the ascendant vascular canals, generally occur in groups, each group corresponding to a polygonal area. The number of ascendant canals in each such group may be only one or a few, but mostly it seems to be rather great. When there are only one or a few of them, these canals pass rather perpendicularly upwards through the central part of their polygonal area. When they are numerous, on the other hand, they enter the basal parts of the exoskeleton rather irregularly scattered beneath their polygonal area. In the latter case, however, they converge rapidly, so that during their further course in a superficial direction they soon reach a rather central position in relation to their polygonal area (pls. 69, 70). The further branching and relation of the vascular canals within the exoskeleton will be dealt with below.

In accordance with HUXLEY (1858) and LANKESTER (1868—1870), we may in the exoskeleton distinguish three layers, which are as follows: the basal layer, the middle layer and the superficial layer.

The basal layer (*bl*, pls. 63—67) is thickest along the anterior and lateral borders of the shield and on the cornua. Further it varies somewhat in relative thickness in different species, and so far as at least the Spitsbergen material is concerned it may perhaps as a whole be thinner in the Devonian forms than in the Downtonian ones. As described by HUXLEY and LANKESTER, it consists of thin fibrous laminae and has numerous cell spaces which always lie between the laminae and which, as a rule, are somewhat flattened. The fibres in each lamina are arranged in such a way that they are nearly at right angles to those in the laminae next above and below. The basal layer is thus composed of true laminated bone.

From what has been pointed out above concerning the subaponeurotic vascular plexus, it is quite obvious that this, when it is enclosed in the exoskeleton, must lie within, or within and just beneath, the basal parts of the basal layer. Moreover from the facts given above concerning the branches from that plexus it is quite clear that the basal layer is traversed by the ascendant vascular canals. These canals seem in most places to branch very sparesely within the basal layer, so that this, as a rule, was comparatively poor in vessels in its interior. Neither in the basal nor in the middle layer I have been able to find any certain evidence of the canals which, according to LANKESTER (1868—1870, pl. 14, fig, 7), would encircle the polygonal areas rather deep down within the exoskeleton. The basal layer, as we shall see, is continuous with and passes directly over into the perichondral bone-layers.

On reaching the middle layer of the exoskeleton the ascendant vascular canals of each polygonal area at once begin to branch frequently (pls. 63—67). The first branches which can be distinguished are sent off in a plane more or less parallel with the external surface of the exoskeleton (*rad.c*, pls. 64—67, 69, 70) and radiate from the central part of their poylgonal area beneath the interareal groovos to the central parts of the four to six neighbouring polygonal areas. When the outer parts of the exoskeleton are split off or removed as deep as to these canals, which will be termed the radiating canals, we get figures like those shown in pl. 70, fig. 2. Since the radiating canals are most numerous in the peripheral parts of the polygonal areas and beneath the interareal grooves, these parts are much weakened so that they are easily exposed both to weathering (in which case the conditions appear as seen in pl. 70, fig. 1), and to breaking, in which case the polygonal areas will appear as more or less independant osseous plates. The radiating canals are in communication with each other by numerous short branches; and from the radiating canals there also issue a great number of other branches outwards, the external branches (*ebc*, pls. 64—67, pl. 72, fig. 3), which form a more or less complex network with eath other, a network which is situated outside the radiating canals and which will be termed the subepidermal vascular plexus. Certain of the external branches may perhaps open into the interareal grooves, which, according to what has been said here, reach into the exoskeleton only as deep as into the middle layer (*iag*, pl. 64, fig. 2).

As is obvious from the facts given here, the middle layer of the exoskeleton (*ml*) is characterized in the first place by the abundant branching of the vascular canals. It thus appears in section only as an irregular mass of trabecles separated by a great number of vacuities. In addition, it differs from the basal layer by its more indistinct lamination and by the circumstance that it has few or no cell-spaces. (I have, however, seen sections in which the cell-spaces are numerous in the middle layer too). Along the lateral and anterior margins of the shield it gradually passes over basally into the basal layer while in most other places its transition into that layer takes place rather suddenly (pls. 63—67). Finally, attention should here also be called to the fact that in several of the forms from the Spitsbergen Devonian it may perhaps have been in a reduced state.

The superficial layer (*sl*) forms a continuous whole only in those forms in which there are no interareal grooves, or at least in which no such grooves are visible from the outside, and, as far as I can judge, it has in these always a smooth shining external surface which is perforated by numerous fine circular pores (pl, 31, fig. 1; pl. 68, figs. 1—3; pl. 70, fig. 2). As far as I can see, these pores are the external openings of certain of the external branches from the radiating canals, that is to say branches from the subepidermal vascular plexus. In those cases where the interareal grooves are distinctly developed, the superficial layer may be found rather differently developed in different species. Thus it may in several species be a continuous covering on each polygonal area, a covering which, just as in the forms without interareal grooves, is smooth and shining externally and perforated by numerous pores (pl. 71, fig. 1). In other species it may be continuous too, but thickened in places, so as to form tubercles. Also in this case it is perforated by numerous pores, but the tubercles exhibit fewer pores than the intervals between them (pl. 40, fig. 1). Finally, in a great many species the superficial layer is absent between the tubercles, so that the middle layer is visible in the intervals. In this case also the tubercles are perforated by rather wide external branches from the subepidermal vascular plexus (*dc*, pl. 72, fig. 3). Further in the species pertaining to the last category the middle layer often seems to be very thin. Especially when the tubercles are sparse, the middle layer seems to be represented almost solely by the radiating canals, the external branches from the radiating canals being few and short and the subepidermal vascular plexus thus almost entirely absent (pl. 66, fig. 1; pl. 67, fig. 1).

The superficial layer consists of dentine: ortho-dentine and osteodentine (pl. 64, fig. 1; pl. 67, fig. 2; pl. 72, fig. 3)[1], which, as the dentine-

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[1] The osteo-dentine is especially to be found in the large tubercles, which occur on the ventral rim, along the margins and on the cornua.

canals diminish in diameter distially acquires an enamel-like appearance. And in fact it seems to me fully correct to consider the most superficial parts of it as enamel, at least in the cases when the external surface is distinctly shining. This enamel, which is perforated by the most peripheral very narrow branches of the dentine-canals, agrees in its structure very well with the enamel occuring in fishes (TOMES 1923). The enamel is of course also perforated by the comparatively much wider external branches from the radiating vascular canals.

The boundary between the superficial and middle layers is often very difficult to observe in the Spitsbergen material, a fact which is fully evident from the microphotographs reproduced in pls. 64—67. In certain cases, however, pulp-like cavities are to be seen below the superficial layer (pl. 67, fig. 2; pl. 72, fig. 3.) just as described by HUXLEY. From these pulp-like cavities, which are merely somewhat widened parts of the external branches from the radiating canals, the dentine canals issue.

In *Cephalaspis hoeli*, and other species in which the superficial layer forms a more or less continuous whole, the external branches from the radiating canals that perforate it may on the ventral rim and on the ventral sides of the cornua (pl. 68, figs. 1—3) be arranged in longitudinal rows. When this is the case, a section transversal to the longitudinal rows will, as shown in pl. 67, fig. 2, exhibit a structure which is very suggestive of *Pteraspis*. And in fact, as I am going to point out in another place in this work, the difference between the Cephalaspids and Pteraspids with regard to the microscopic structure of the exoskeleton seems not to be of any deep nature.

From its minute structure it is easy to conclude that the exoskeleton — except the most superficial part of the superficial layer, which was formed by the epidermis — must have arisen in the corium. And in addition it is also easy to see that it must have occupied the corium in its entire thickness.

Before leaving the typical Cephalaspids the conditions in *Thyestes verrucosus* deserve a closer attention. In that species the superficial layer is restricted merely to the tubercles which, as is well known, are rather sparse (cf. pl. 48, fig. 1 in the present work). On account of this the middle layer forms a comparatively great part of the exposed external surface. There are no traces of interareal grooves, a fact which seems to me to indicate that the external parts of the middle layer had become reduced, so that the structures which, as we shall see, were lodged in the interareal grooves probably — if they had not been reduced too — must have been situated entirely in soft tissue. In full accordance with this view is the fact that the middle layer is rather thin (cf. ROHON 1896 b, pp. 229—232). As pointed out above (p. 36) conditions more or less similar to those now described in *Thyestes verrucosus* with regard to the external parts of the exoskeleton occur also in certain other Cephalaspids in which the superficial layer is restricted merely to tubercles which occur at great intervals from each other. — In certain of the forms from the Devonian of Spitsbergen the external layer may perhaps be still more reduced than in *Thyestes* or perhaps even entirely absent.

For the sake of comparison we shall now turn to *Tremataspis*. In this form the exoskeleton may, as in the typical Cephalaspids, be considered to consist of three layers: a basal one, a middle one and a superficial one (Pl. 72, figs. 1, 2; cf. PATTEN 1912, pp. 290—292; figs. 193—195)[1].

The basal layer, which consists of laminated bone, always rich in cell-spaces, is very thick and distinguished from that in Cephalaspids in general by the presence of numerous big cavities (*ms*) in its interior. From each such cavity there leads a canal basally to the basal side of the exoskeleton and a canal (*sc*, pl. 72, figs. 1, 2) superficially into the middle layer. As far as can be seen, the basal layer was almost smooth on the basal side, i. e. it exhibits no traces of having enclosed any subaponeurotic vascular plexus.

The middle layer is considerably thinner than the basal one. Like that, it consists of laminated bone and contains numerous canals which branch abundantly. As has been pointed out by PATTEN (1912 loc.cit) these canals are of two different categories, vascular ones and ones which probably were mucous or had some sort of sensorial function.

The former of these canals (*rad.c*, pl. 72, figs. 1, 2) are all rather narrow and run almost parallel with the external surface just beneath the superficial layer, forming a thin plexus there (very well displayed in surface view in pl. 72, fig. 2, right lower corner) with their anastomoses. Three, four or sometimes still more of them unite basally into wider canals, which penetrate in a basal direction, forming the canals (*sc*) which issue from the superficial side of the big cavities in the basal layer. As is seen from their course and arrangement therefore, there can be no doubt that the canals of the middle layer just described really are vascular canals and that the big cavities in the basal layer lodged vessels too. The plexus formed by the vascular canals beneath the superficial layer evidently corresponds to the subepidermal vascular plexus of the typical Cephalaspids.

The other canals of the middle layer of *Tremataspis*, which for the sake of brevity will be referred to as the mucous canals (*mc*, pl. 72, figs. 1, 2), are situated slightby deeper than the subepidermal vascular

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[1] The descriptions of the exoskeleton of *Tremataspis* given by ROHON are in several important respects incorrect and owing to that they have not been discussed here.

plexus, forming, however, with each other a plexus too (well shown in pl. 72, fig.2). They are considerably wider than the vascular canals and open outwards with wide, short branches, which perforate the superficial layer. Each such branch, which leads to the external surface of the bone, seems to be situated about in the centre of a mesh of the subepidermal vascular plexus (pl. 72, fig. 2). In certain places I have seen branches from the vascular system opening into the mucous canals on the basal side, a state of things which shows that the mucous canals received vessels and nerves through the vascular canal system. As emphasized by PATTEN, however, the communications between the two categories of canals are rather sparse. Everything that is known of them so far is thus apparently in favour of the view advanced here that the canals described as mucous ones cannot have been vascular canals but must have had some other function. Whether this was simply a mucous one or some sort of sensorial one must remain undecided at present.

Before proceeding further in our description of the conditions in *Tremataspis* it will be of importance to observe a little more in detail certain relations of the mucous canals exposed in pl. 72, fig. 2. At the place denoted by *c* we see a rather small quadrangular area encircled by thick and strong mucous canals. At *a* we find similar areas but with the difference that these areas are bounded by thick mucous canals only on two sides, the other two sides being bounded by narrow mucous canals, which appear to have developed secondarily. In fact we find at *a*, four equally small areas, which obviously form parts of a single large area, bounded entirely by thick mucous canals; and accordingly we have here an area which seems to be secondarily subdivided. At *b* and *d* we find indications of similar large areas secondarily subdivided into smaller ones. Since now in each such large area there ascend from below four, five or six or perhaps even more vascular canals (branches from the canals *sc*) arranged in a somewhat regular way around the centre, and these vascular canals penetrate in a superficial direction, branching, and forming a subepidermal vascular plexus it seems to me very conceivable that the large areas surrounded by thick mucous canals in fact correspond to the polygonal areas of the typical Cephalaspids, and that consequently the mucous canals of ***Tremataspis*** are represented in the Cephalaspids by the interareal grooves.

Finally the superficial layer of the exoskeleton of *Tremataspis* forms, as we know, a continuous covering on the middle layer. It is limited basally by the subepidermal vascular plexus, from which numerous fine canaliculi issue in a superficial direction into it, penetrating as far as to the external surface on which they open with fine pores (pores of this sort seen as fine black dots in the right lower corner of fig. 2, pl. 72). These canaliculi frequently anastomoze with each other by fine branches and are in several places somewhat expanded, so that spaces are formed, which are very similar in size and shape to the cell-spaces in the two other layers, and which perhaps lodged cells (cf. PATTEN 1912, fig. 195, p. 292). If this really was so, if these small spaces really were cell-spaces, we should be concerned here with a very peculiar sort of tissue, since its character otherwise is chiefly dentine-like. We should in fact have a tissue occupying complete intermediary conditions between true bone and dentine. The most superficial part of the superficial layer, which forms the smooth, shining external surface of the cephalic shield, probably consisted of enamel or of a tissue closely resembling that.

From what has been now set forth, therefore, it seems as if the subdivision of the external parts of the exoskeleton of the Cephalaspids into polygonal areas is not due to a coalescence of small polygonal bone plates, as has hitherto often been supposed. The interareal grooves of the Cephalaspids would only be the markings or impressions of structures corresponding to the so-called mucous canals of ***Tremataspis.*** These mucous canals would thus in the Cephalaspids to a considerable extent have been situated in soft tissue. In such forms as ***Thyestes verrucosus***, with the middle and superficial layers much reduced, they seem even to have lain entirely in soft tissue, so that there are no impressions of them on the exoskeleton.

After this description of the exoskeleton we turn next to the endoskeleton. In *Boreaspis rostrata*, in which, as we have seen, the endoskeleton is ossified throughout, I have not studied the minute structure of it, since the available material of this species is too limited to be used for microscopic sections. In the other forms, in which, as described above (p. 30), the endoskeleton was cartilaginous but provided with perichondral bone-layers, I have had several opportunities of studying the finer structure of these perichondral bone-layers, and I have found that they all consist of laminated bone of the same type as the basal layer of the exoskeleton. Most of the perichondral layers, however, are very thin and composed only of a few laminae.

It has already been mentioned that the perichondral bone layers are continuous with the exoskeleton. More closely defined, they are continuous with and pass over only into the the basal part of the basal layer of the exoskeleton, with which as we have found, they agree completely in structure. These conditions seem to me, at least to a certain extent, to lead to the suspicion that the basal layer of the exoskeleton most basally may include certain laminae formed by the perichondrium of the underlying endoskeleton and that accordingly the most basal part of the basal layer of the exoskeleton in fact may be of an endoskeletal origin. This suspicion is further supported by the fact that as set forth above the subaponeurotic vascular plexus is often found included in the basal parts of the basal layer.

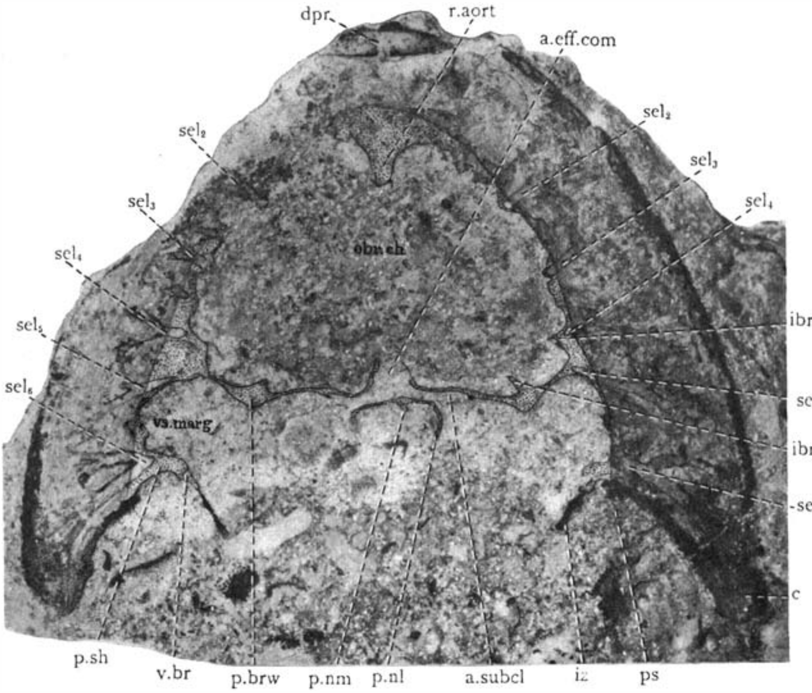
There are thus certain facts which seem to indicate that what has been termed exoskeleton in the Cephalaspids in its most basal part perhaps may not be of a purely dermal origin. A fully positive decision in this question will hardly be possible, however, since we cannot study the ontogeny of the exoskeleton.

The oralo-branchial chamber and the postbranchial wall.

On the lower side of the cephalic division proper of the cephalic shield we find, as already described above, the large oralo-branchial fenestra (text-figs. 1 B, 4, 8 B), which, as has also been mentioned was closed, except for the mouth opening and the branchial openings, by soft tissue, which may have contained one or more cartilages and which was strengthened externally with scales or a number of scale-like plates (cf. pp. 20—21 above; cf. also the chapter on the visceral skeleton below). As has also been pointed out, this fenestra leads upwards into the extensive oralo-branchial chamber, a space in which in the mouth cavity, the pharynx and the gill-sacs were situated. I shall here give a brief account of that chamber and its boundaries.

The oralo-branchial chamber (*obr. ch*, text-figs. 2, 4, 9—13; pls. 15, 44, 51, 52) is situated entirely within the endoskeletal component of the cephalic shield, its dorsal boundary beeing formed by the endocranial part of the endoskeletal component, its anterior, lateral and posterior boundaries, on the contrary, by the visceral part of the same component. Its ventral boundary was, as is easily understood, the soft tissue that closed the oralo-branchial fenestra; and, with the exception of the ventral side, it was lined throughout by the external perichondral bone-layer. It is widest and longest most ventrally, immediately above the oralo-branchial fenestra, diminishing rapidly upwards both in longitudinal and transversal extensions. Its maximum breadth, is situated beneath the ethmoidal, orbitotemporal and otic regions of the endocranium.

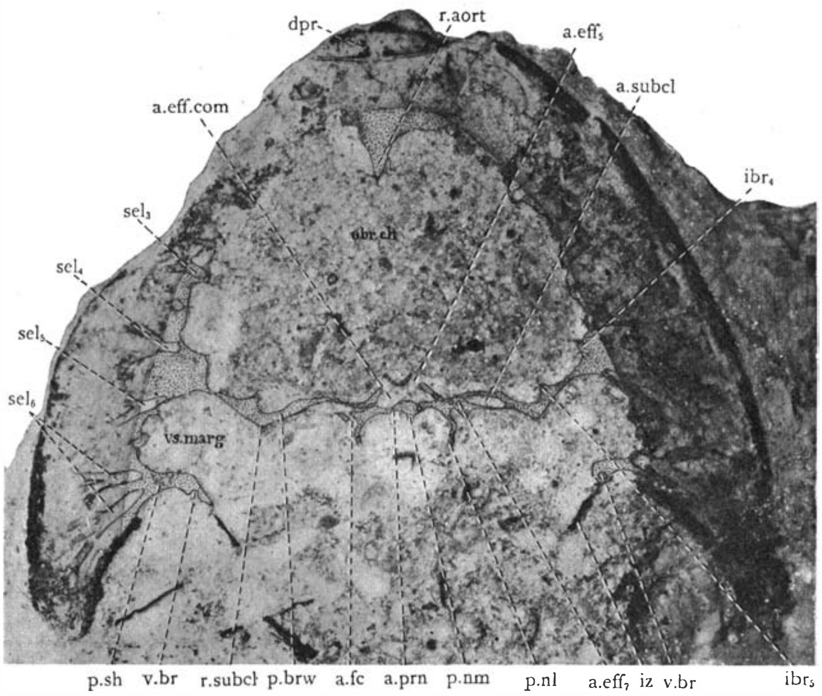
The posterior boundary of the oralo-branchial chamber — that is to say, the posterior portion of the visceral part of the endoskeleton — is a wall which descends from the ventral side of the endocranial part of the endoskeleton in a postero-ventral direction; and, as this wall reaches so far downwards and posteriorly as the inside of the exoskeleton following behind the oralo-branchial fenestra it forms a complete septum between the oralo-branchial chamber and the trunk (*p. brw*, text-figs. 2 A, 4, 9—12, 13, 33—35; pls. 8—10, 14, 15, 20, 22, 23, 42; pl. 46 fig. 1; pl. 47 fig. 1; pls. 49—58). More exactly, it descends from the neurocranium



Text-fig. 9. *Cephalaspis hoeli*. Cephalic shield in dorsal aspect but with the most dorsal parts removed by grinding. Bone layers appearing as black lines. The parts of endoskeleton which consisted of cartilage denoted by dotting. Magnification about $^{3}/_{1}$.

a. eff. com, canal for the arteria branchialis efferens communis, a vessel formed by the confluence of the efferent branchial arteries 4—6; *a. subcl*, canal for the arteria subclavia; *c*, cornu; *dpr*, area which bounded the mouth cavity on the dorsal side; *iz*, lateral wall of the interzonal part of the trunk division of the cephalic shield. (It is clearly seen here that it consists solely of dermal bone); ibr_4, ibr_5, interbranchial ridges 4 and 5; *obr. ch*, oralo-branchial chamber; *p. brw*, postbranchial wall; *p. nl*, thin lamina from the postbranchial wall for the protection of the pronephros on the lateral side; *p .nm*, sagittal lamella dividing the pronephros space into right and left halves; *ps*, pectoral sinus; *p. sh*, endoskeletal shoulder girdle; *r. aort*, ridge for the most anterior part of the aorta; sel_2—sel_6, canals for the nerves 2—6 to the lateral electric field; *v. br*, canal probably for the v. brachialis; *vs. marg*, marginal vein sinus.

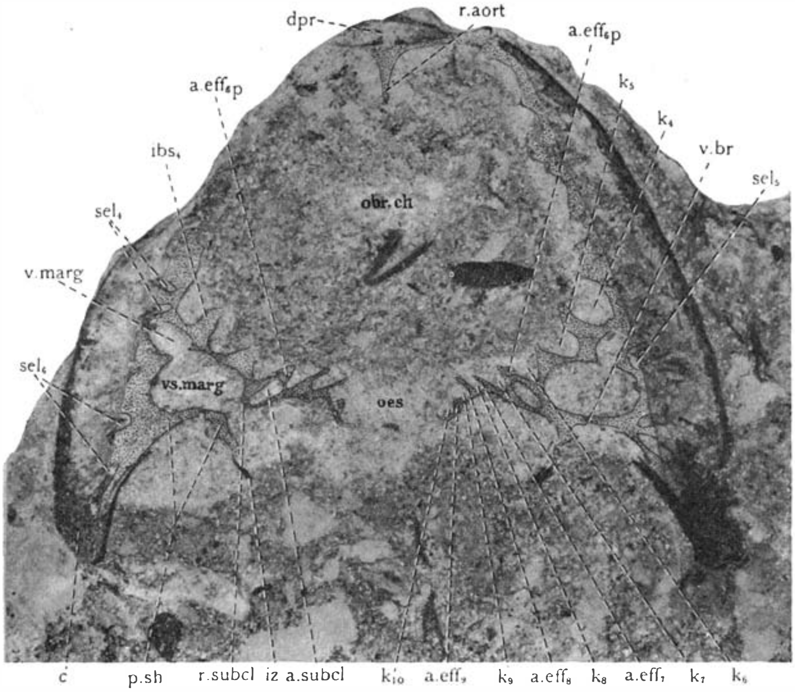
about at the transition between the otic and occipital regions, the latter region thus falling behind the oralo-branchial chamber. It has already been observed by several of the scientists who have preveously dealt with Cephalaspids and with *Tremataspis* (Egerton 1857; Lankester 1868—1870; Woodward 1891 a; Rohon 1896 b; Jaekel 1903, 1921; Wiman 1918 etc.), though its true nature has not before been understood. Since it must be frequently referred to in this work, it will for practical reasons be necessary to introduce a special term for it; and as has already been mentioned above (p. 31), I have called it the postbranchial wall.



Text-fig. 10. *Cephalaspis hoeli.* Cephalic shield in dorsal aspect. Certain dorsal parts removed by grinding; and somewhat more has been removed than in text-fig. 9. Bone-layers in section appearing as black lines. The parts of the endoskeleton which consisted of cartilage denoted by dotting. Magnification about 3/1.

a. fc, canal for an artery arisen by the confluence of the efferent branchial arteries 8 and 9; *a. eff. com*, canal for the arteria branchialis efferens communis, a vessel formed by the confluence of the efferent branchial arteries 4—6; *a. eff*$_5$, *a. eff*$_7$, canals for the arteriae branchiales efferentes 5 and 7; *a. prn*, canal for a small branch from the arteria branchialis efferens communis to the pronephros space; *a. subcl*, canal for the arteria subclavia; *dpr*, area which bounded the mouth cavity on the dorsal side; *iz*, lateral wall of the interzonal part of the trunk division of the cephalic shield (it is clearly seen here that it consists solely of dermal bone); *ibr*$_4$, *ibr*$_5$, interbranchial ridges 4 and 5; *obr. ch*, oralo-branchial chamber; *p.brw*, postbranchial wall; *p. nl*, thin lamina from the postbranchial wall for the protection of the pronephros on the lateral side; *p. nm*, sagittal lamella dividing the pronephros space into right and left halves; *p. sh*, endoskeletal shoulder girdle; *r. aort*, ridge for the most anterior part of the aorta; *r. subcl*, subclavian ridge; *sel*$_3$—*sel*$_6$, canals for the nerves 3—6 to the lateral electric field; *v. br*, canal probably for the v. brachialis; *vs. marg*, marginal vein sinus.

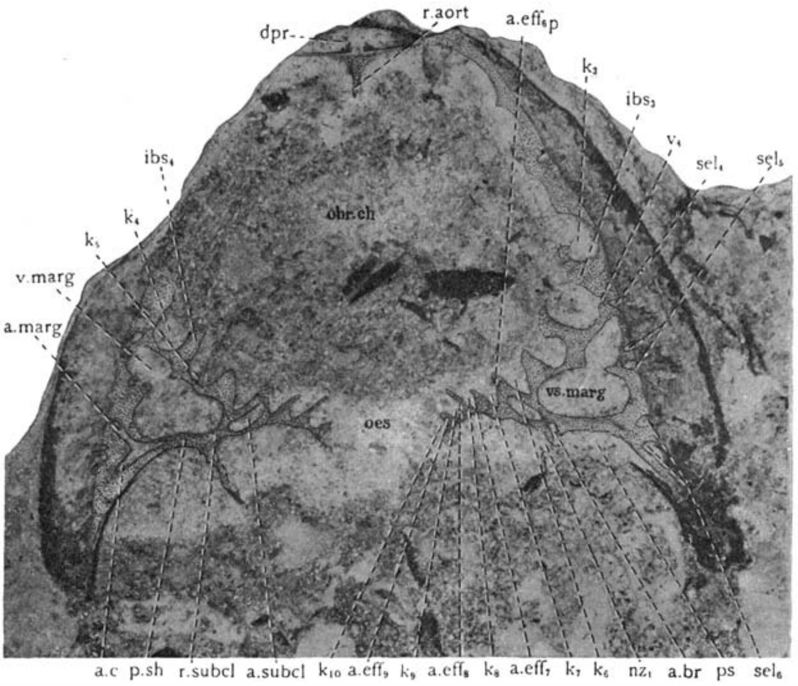
The postbranchial wall, as thus defined, was in *Boreaspis rostrata* ossified throughout. In the other Spitsbergen forms it consisted of cartilage which was lined, both on the anterior and on the posterior sides, by the external perichondral bone-layer. As seen from text-figs. 9—12 and pls. 23, 53, 56, it is thickest in the lateral and dorso-medial parts. In *Kiaeraspis*, *Boreaspis rostrata*, and perhaps in other forms too, it is perforated by a big median unpaired foramen for the oesophagus (*oes*,



Text-fig. 11. *Cephalaspis hoeli.* Cephalic shield in dorsal aspect. Same specimen as in text-figs. 9 and 10 but still more of the dorsal parts removed. Bone layers in section appearing as black lines. The spaces occupied by cartilage dotted. Magnification about 3/1.

a. eff$_6$p, canal for a vessel, probably an artery from the posterior, half of the sixth branchial fossa to the canal for the a. subclavia; *a. eff*$_7$—*a. eff*$_9$, grooves for the efferent branchial arteries 7—9; *a. subcl*, canal for the a. subclavia; *c*, cornu; *dpr*, area which bounded the mouth cavity on the dorsal side; *ibs*$_4$, interbranchial septum 4; *iz*, lateral wall of the interzonal part of the trunk division of the cephalic shield; k_4—k_{10}, branchial fossae 4—10; *obr. ch*, oralo-branchial chamber; *oes*, foramen for the oesophagus; *p.sh*, endoskeletal shoulder girdle; *r. aort*, ridge for the most anterior part of the aorta (imperfectly preserved); *r. subcl*, subclavian ridge; *sel*$_4$—*sel*$_6$, canals for the electric nerves 4—6 to the lateral electric field; *v. br*, canal for the brachial vein; *v. marg*, canal for the marginal vein; *vs. marg*, marginal vein sinus.

text-fig. 4; pls. 15, 52, 53, 58) and below that by a somewhat smaller foramen (*tr*), which is unpaired too and which transmitted the truncus arteriosus. This latter foramen always lies very low. In the *Cephalaspis*-species in which they could be studied these two foramina are, on the contrary, incompletely separated from each other, forming there a single big foramen subdivided into a dorsal wide division for the oesophagus and a ventral more narrow division for the truncus arteriosus (*oes*, *tr*, text-figs. 2, 11, 12 — in 11 and 12 only the oesophageal division seen in sections — 33, 34, pls. 9, 10; pl. 23, fig. 1). In all forms the postbranchial wall is perforated not only by the foramina now described



Text-fig. 12. *Cephalaspis hoeli.* Cephalic shield in dorsal aspect. Same specimen as in text-figs. 9—11, but still more of the dorsal parts removed by grinding. Bone-layers in section appearing as black lines. The spaces occupied by cartilage dotted. Magnification about $^3/_1$.

a. br, canal for the arteria brachialis; *a. c*, canal for the arteria cornualis; *a. eff*$_6$p, canal for a vessel, probably an artery, from the posterior half of the sixth branchial fossa to the canal for the a. subclavia; *a. eff*$_7$—*a. eff*$_9$, grooves for the efferent branchial arteries 7—9; *a. marg*, canal for the arteria marginalis; *a. subcl*, canal for the a. subclavia; *dpr*, area which bounded the mouth cavity on the dorsal side; *ibs*$_3$, *ibs*$_4$, interbranchial septa 3, 4; *k*$_3$—*k*$_{10}$, branchial fossae 3—10; *nz*$_1$, canal for a vein from and perhaps also for a nerve to the pectoral fin; *obr. ch*, oralo-branchial chamber; *oes*, foramen for the oesophagus; *ps*, pectoral sinus; *p. sh*, endoskeletal shoulder girdle; *r. aort*, ridge for the most anterior part of the aorta (imperfectly preserved); *r. subcl*, subclavian ridge; *sel*$_4$—*sel*$_6$, canals for the electric nerves 4—6 for the lateral electric field; *v*$_4$, canal for the fourth ventral transversal superficial vein; *v. marg*, canal for the marginal vein; *vs. marg*, marginal vein sinus.

but also by several much finer ones for nerves and vessels, that will be dealt with below in another connection.

In the roof of the oralo-branchial chamber the Cephalaspids have a broad median rostro-caudally running ridge (*r. aort*, text-figs. 4, 9—13, 33; pls. 13—15; 17, 18, 21, 22; pl. 23, fig. 3; pl. 29; pl. 33, fig. 1; pl. 37, fig. 1; pl. 44; pl. 46, fig. 1; pls. 51, 52, etc.), which from the postbranchial wall extends forwards until somewhat behind the rostral end of the oralo-branchial chamber, more exactly until the posterior end of the somewhat excavated area denoted in the figures by the letters *dpr* (text-figs. 4, 9—13, 36; pl. 40, fig. 4; pl. 51). This ridge is grooved in its longitudinal direction, and the groove certainly lodged the cephalic portion of the dorsal aorta, which thus was unpaired here. According to their function the ridge and the groove may be referred to as the aortal ridge and the aortal groove respectively. Posteriorly the aortal groove, as thus defined, leads to a canal through the most dorsal part of the postbranchial wall, a canal which will be further dealt with below in another connection. The anterior opening of this canal is distinctly seen in text-figs. 4 and 33.

On each side of the aortal ridge the roof of the oralo-branchial chamber is somewhat bulged downwards by the auditory organ and by the orbit, so that we find on it a paired distinct otical prominence (*pr. au*, text-figs. 4, 13, 33, 36; pls. 20, 23, 44, 46. 51—58) and a likewise paired, also distinct orbital prominence (*pr. orb*, figs. cit.). These two prominences of each side are separated by a shallow transverse groove, the orbitootical groove (*orb. ot. gr*, text-fig. 4, 13); and anteriorly to the orbital prominence of each side there may sometimes be a rather pronounced fossa, which, according to its position ventrally and somewhat laterally to the olfactory organ, may be called the subnasal fossa (*f. sn*, text-figs. 4, 13). Especially in several *Cephalaspis*-species this fossa is distinctly developed (pl. 20; pl. 23, fig. 3, pl. 29).

A very striking feature of the oralo-branchial chamber is that its lateral and posterior surfaces are provided with deep dorsi-ventrally extended fossae (k_1—k_{10}, text-figs. 4, 11, 12, 33, 36, 39, 40) separated by septa (*ibs*) ventrally and by low ridges (*ibr*) dorsally. These fossae, which as a rule are 10 in number on each side of the median line, reach from the aortal ridge downwards almost to the ventral margin of the oralo-branchial chamber, and are, as is seen, rather deep in their ventral parts. The anterior ones of them always have a more or less transversal arrangement in relation to the longitudinal axis of the head, while the posterior ones, on the contrary, may gradually change their position in certain forms, so that they get a more rostro-caudal direction. Since it cannot be doubted that all these fossae must have been caused by the respiratory apparatus they may be termed branchial fossae, while the septa and ridges separating them may be referred to as interbranchial septa and interbranchial ridges respectively.

Already in this connection it should be pointed out that from the appearance of the branchial fossae, interbranchial septa and interbranchial ridges it is fully evident that the respiratory apparatus cannot have been like that in fishes, but instead like that in Cyclostomes, i. e. it must have consisted of more or less sac-like gills.

The somewhat excavated area *dpr*, (text-figs. 4, 9—13; pl. 40, fig. 4; pls. 44, 51; section series D, nos. 45, 49), which has already been referred to above, is present in all forms and, as we shall see, it is beyond question that it formed part of the roof of the mouth.

Further details concerning the oralo-branchial chamber and the different structures related to it will be given below in connection with the descriptions of the endocranium and the visceral endoskeleton.

The Head.

General shape of the head.

The head of the Cephalaspids is broad and always more or less depressed in dorsi-ventral direction (text-figs. 1—6). Its ventral side is slightly convex or almost flat. Its dorsal side, on the contrary, is rather high in its posterior median parts, but slopes rather rapidly from there both forwards towards the rostrum and laterally towards the lateral borders, the height thus being very inconsiderable along the anterior and lateral borders.

As has already been pointed out, the orbital openings are situated on the dorsal side of the head, rather close to each other. Between them lies the pineal foramen and slightly anteriorly to that the unpaired nasal opening. The mouth-opening and the external openings of the gills-sacs were situated on the ventral side.

Endocranium.

From the general description given above we have seen that the cephalic shield consists not only of exoskeleton (dermal bone) but also of a very considerable endoskeletal component. It has also been pointed out that the latter component or, as it is called here, the endoskeleton is a very complex structure, including not only the endocranium but also considerable dorsal parts of the visceral endoskeleton and the entire endoskeletal shoulder girdle, which all are continuous with each other.

On account of these very peculiar conditions, of course, it would be most correct to treat the endoskeleton as a whole; but for practical reasons I have preferred not to do so. Instead I shall describe the different parts of it quite independently of each other, a procedure which, in my opinion, renders it more easy to compare the Cephalaspids with other lower vertebrates in which normal conditions prevail.

It is impossible to decide exactly where the boundaries may be drawn between the endocranium on the one hand, and the visceral endoskeleton and the endoskeletal shoulder-girdle with which it is continous, on the other hand; and owing to this we can only say that the endocranium with regard to its general shape was as a whole rather broad.

As we have found, the endocranium was either entirely ossified (*Boreaspis rostrata*) or consisted of cartilage lined externally and in all cavities and canals with perichondral layers of bone (most Cephalaspids). That the cartilage, when it was present, perhaps was of a sort resembling the mucous cartilage of the larvae of the recent Petromyzontids has also been mentioned (cf. p. 30; cf. also the comparison between the Cephalaspids and the Petromyzontids below).

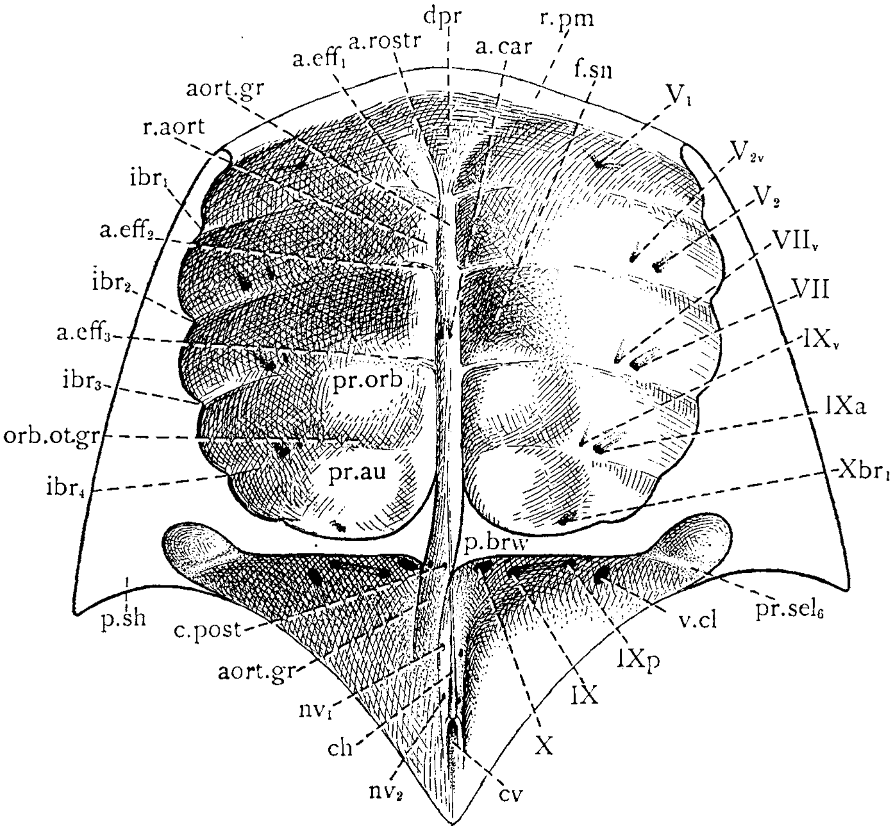
In the endocranium we may distinguish occipital, otic, orbitotemporal and ethmoidal regions as normally among craniate vertebrates.

In this connection it should also be mentioned that between the endoskeleton and the exoskeleton there is, as pointed out above, a vascular plexus which, owing to is position just beneath the corium-aponeurosis, was called the subaponeurotic vascular plexus.

Occipital region. — The occipital region (text-figs. 7, 8, 13, 14; section series A nos. 1—55; section series B, nos. 1—17; section series C, nos. 1—105) is always rather long as compared with the other regions of the endocranium, but it varies a great deal in length in different forms according to the length of the trunk-division of the cephalic shield. Thus it is much longer in *Kiaeraspis* (text-fig. 8; pl. 54, fig. 1) — in which as we have seen the trunk-division of the cephalic shield is long — than in *Cephalaspis* (text-figs. 7, 13; pl. 23, fig. 3) or *Hoelaspis* (pls. 44, 45) in both of which the trunk-division of the cephalic shield is short. In dorsal or ventral view it has approximately the shape of an isoscelous triangle, with the base forwards and continuous with the otic region and the point backwards, thus being broad anteriorly and decreasing rather rapidly in breadth backwards. Most anteriorly it is continuous on the ventral side with the median part of the postbranchial wall and laterally on each side with the endoskeletal shoulder-girdle. Owing to this connection with the endoskeletal shoulder-girdle, therefore, its lateral borders become free only behind the endoskeletal shoulder-girdle. The lateral extension of the part of it that projects freely backwards behind the endoskeletal shoulder-girdle is well displayed in the specimen of *Cephalaspis hoeli* figured in pl. 23, fig. 3 (the line denoted by the letters *olm* indicates the position of the free lateral margin of the region).

Taken as a whole, the occipital region is low in relation to its breadth (section series A, nos. 1—50). Its lateral parts are curved slightly downwards, causing its upper surface to be convex and its lower surface to be correspondingly concave in a tranverse direction. Since the lateral parts gradually diminish in height laterally until they become very thin, the free lateral borders are almost edge-shaped.

We first turn to the ventral surface. As has been pointed out above, this is lined by the external perichondral bone layer. On it there is, above all, to be noticed a strong, median, longitudinal ridge,



Text-fig. 13. *Cephalaspis sp.* Diagrammatic sketch of the endocranium in a ventral view. The postbranchial wall and the visceral endoskeleton to a large extent removed. Section areas white, without any shading.

a.car, canal for the carotid artery (paired); *a.eff*$_1$—*a.eff*$_3$, grooves for the efferent branchial arteries 1—3; *aort.gr*, aortal groove; *a.rostr*, groove for the rostral artery (premandibular efferent branchial artery); *ch*, notochordal groove; *c.post*, canal for the posterior encephalic artery; *cv*, cavum cerebrale cranii (posterior end); *dpr*, area which bounded the mouth cavity on the dorsal side; *f.sn*, fossa subnasalis; *ibr*$_1$—*ibr*$_4$, interbranchial ridges 1—4; *nv*$_1$, *nv*$_2$, canals for the myelonal arteries 1, 2 and in addition probably for the ventral roots of the first and second spino-occipital nerves; *orb. ot. gr*, orbito-otical groove; *p. brw*, postbranchial wall (in section); *pr. au*, otical prominence; *pr. orb*, orbital prominence; *pr. sel*$_6$, ridge caused by the canal for the sixt electric nerve to the lateral electric field; *p. sh*, endoskeletal shoulder-girdle; *r. aort*, aortal ridge; *r. pm*, prebranchial ridge; *v. cl*, canal for the vena capitis lateralis (posterior opening); V$_1$, canal for the n. profundus; V$_2$, canal for the n. trigeminus proper; V$_{2v}$, canal for the visceral branch of the n. trigeminus proper; VII, canal for the n. facialis; VII$_v$, canal for the visceral branch of the n. facialis; IX, branch of the vagus canal through which the n. glossopharyngeus had its exit behind the postbranchial wall; IX *a*, canal for the n. glossopharyngeus through the otic region to the oralo-branchial chamber; IX$_p$, posterior canal for n. glossopharyngeus through the otic region; IX$_v$, canal for the visceral branch of the n. glossophcryngeus; X *br*$_1$, canal for the first branchial branch of the n. vagus; X, vagus branch of the vagus canal for the branchial branches and for the n. linae lat. and the r. intestinalis.

which lodges the occipital division of the cavum cerebrale cranii and which may therefore be called the neural ridge (text-fig. 13; cf. also pl. 23, fig. 3 and pls. 49, 53—57; and section series A, nos. 1—55). This ridge extends from the transition between the occipital and otic regions rather far backwards on the latter region, but never as far as the posterior end of it. Almost throughout its length it is of a rather uniform width, only its most anterior parts being wider than the others. Its posterior end reaches in the fossils considerably farther backwards with its most dorsal parts than with its ventral ones. Consequently the posterior opening of the cavum cerebrale cranii, the foramen magnum, as found in the fossils, occupies a very oblique position, so that it faces very much downwards (text-fig. 13). Since in the living forms, at least as far as can be judged from the conditions in a specimen of *Cephalaspis hoeli* (section series A, nos. 8—16), the neural ridge most postero-ventrally had certain entirely cartilaginous parts beneath the ones lined by perichondral bone, the foramen magnum probably lay in these somewhat more posteriorly than it does in the fossils at the same time as it probably faced straighter backwards. Despite the probability that the foramen magnum thus in the living forms may have been situated somewhat differently than in the fossils yet it is quite obvious that there must have been a rather gradual transition between the neural ridge and the vertebral column. The most posterior part of the occipital region behind the neural ridge exhibits on its lower side no traces of having been related to the spinal canal (section series A, nos. 1—8); and it seems therefore likely that it projected freely backwards as a process close above the vertebral column.

On the ventral side of the neural ridge there is a very distinct groove for the notochord (*ch*, text-fig. 13; section series A, nos. 1—55, section series B, nos. 1—7), a groove which cotinues forwards on to the otic region This groove is most posteriorly, where it first appears, rather wide but shallow in proportion to its width, so that it probably cannot have lodged more than approximately the dorsal half of the notochord (section series A, nos. 17—20). Further forward in the region it gradually diminishes in width, most anteriorly at the transition to the otic region, getting very narrow (section series A, nos. 21—55). Simultaneously as it diminishes in width forwards, however, it grows deeper in proportion to the width and gets such a shape that there can be no doubt that the notochord except for a narrow ventro-median strip, was entirely enclosed in it. In the posterior parts of the region it is imperfectly bounded from the cavum cerebrale cranii in the present state of preservation; but in the living forms this was not the case for in these the dural connective tissue — the endorhachis — must of course have lined the entire cavum cerebrale cranii and have formed alone the floor of that cavity in those places in which there was no cartilage or bone ventrally to it. The fact that the notochordal groove most posteriorly was so shallow that it lodged only a dorsal part of the notochord indicates that the posterior parts of the neural ridge is composed only of homologeus to the dorsal vertebral arches. Further forward, on the other hand, where the notochord is almost completely enclosed in the base of the neural ridge, the homologues of the ventral vertebral arches too seem to form part of that ridge.

On the anterior half of the ventral surface of the region a pronounced, unpaired, broad groove is always to be seen (*aort. gr*, text-fig. 13; section series A, nos. 21—55; section series B, nos. 1—12; scction series D, nos. 1—11; pl. 23, fig. 3; pls. 44, 45; pl. 53, fig. 1; pl. 54, fig. 1; pl. 55; pl. 56, fig. 1). With its posterior parts this groove is situated close to, but entirely on the right side of, the neural ridge and thus asymmetrically. Forwards it gradually approaches the median line, thus changing its position in relation to the neural ridge, so that it finally becomes situated on the ventral side of that ridge. On reaching the postbranchial wall it is bridged over ventrally and transformed into a canal (*aort*, text-fig. 2 A, section series B, nos. 1—5; section series C, nos. 17—52), which pierces the postbranchial wall. In front of that wall it is continued by the unpaired median groove in the roof of the oralo-branchial chamber, the groove which was described above (p. 46) as the aortal groove. Hence we find that the dorsal aorta behind the postbranchial wall did not run in the median line in a haemal groove beneath the notochord as it usually does, but that it had an asymmetrical position on the right side of the notochord and the medulla spinalis. In this connection it is of interest to call attention to the fact that an asymmetric disposition of the ductus cuvieri and the big veins leading to this occurs in recent Cyclostomes (CORI, 1906, p. 53; HATTA 1922, p. 174, etc.; for further details see the chapter on the Cyclostomes in the present work).

On the most lateral part of the ventral surface of the region close to the endoskeletal shoulder-girdle, a rather narrow but distinct ridge, caused by the canal for the most posterior nerve to the lateral electric field, goes from the otic region laterally and somewhat backwards to the endoskeletal shoulder-girdle (*pr.* sel_6, text-fig. 13; sel_6, pl. 23, fig. 3; pls. 27, 29, 30).

Finally on the dorsal surface of the region we find the posterior part of the dorsal electric field (*dsf*, pl. 17), which, as is seen from the series of transverse sections of *C. hoeli*, generally reached far backwards (section series A, nos. 11—55; section series B, nos. 1—17).

The conditions of the walls enclosing the occipital division of the cavum cerebrale at different places is so well displayed by the section section series (section series A, nos. 1—55; B, nos. 1—17; C, nos. 1—105; D, nos. 1—42) that no special description is necessary.

The occipital division of the cavum cerebrale cranii (*cv*, text-figs. 2, 13; *med* text-fig. 15—17, 20—28; section series A, nos. 1—55; B, nos. 1—17; C, nos. 1—40; D, nos. 1—29; pl. 18; pl. 19; fig. 1; pl. 23, fig. 3; pls. 25, 26, 44, 45, 48, 49; pl. 53, fig. 1; pl. 54; fig. 1; pls. 55, 57) is, in its posterior half, hardly more than a comparatively fine tube or canal, which is somewhat higher than it is broad, but forwards it increases in both height and breadth — especially, however, in bredth. It attains its greatest dimensions at the vagus exit, i. e. about at the transition to the otic region. Contrary to what is the case further back it is there broader than it is high.

From the occipital division of the cavum cerebrale there issue several canals for nerves and vessels; and among these canals we shall first consider the vagus canal.

The vagus canal of the right side was probably situated slightly further forwards than the one of the left side. Otherwise it is noticeable that the vagus canal seems to vary somewhat with regard to certain of its details not only in different species but also in different specimens of the same species. It is even somewhat different on both sides in the same specimen, a condition which, as it is caused by the asymmetrical position of the aortal groove, probably is rather constant. Unfortunately it could be thoroughly studied only in three specimens of *Cephalaspis hoeli* and in one specimen of *Kiaeraspis* which were all used for sections; but as in all these four specimens it was imperfectly preserved in certain respects, our knowledge of it still remains rather limited.

In *Cephalaspis hoeli* (text-figs. 15—17, 24, 26; section series A, nos. 44—55; section series B, nos. 1—17; section series C, nos. 32—70; section series E, nos. 4—12); it is (IX+X+X*vcp*) at the origin from the cavum cerebrale rather high but narrow in a rostro-caudal direction and situated so that the dorsal part lies somewhat more caudally than the ventral one, i. e. its axis of height is somewhat inclined backwards. It goes for some distance latero-ventrally and slightly posteriorly without giving off any branches, then suddenly dividing into two main branches, a dorsal one and a ventral one, the latter of which in its turn may soon divide more or less distinctly into two branches, a dorsal one and a ventral one. We thus find that the vagus canal of the species in question consists of a proximal undivided, high but narrow division and a distal division, which generally breaks up into three branches.

The most dorsal of these three branches (X*vcp*), which is always rather large, is given off from the dorsal — or more correctly from the postero-dorsal — part of the proximal division of the vagus canal. It goes latero-dorsally and somewhat backwards, opening into the ventro-medial corner of the big occipital vein sinus (*vs. oc*) to be described below. And from its relation to that vein sinus it is fully obvious that it transmitted a vein from the posterior parts of the cavum cerebrale. This vein, which thus traversed the dorsal part of the proximal division, of the vagus canal seems to have corresponded exactly to the similarly running vena cerebralis posterior (v. encephalica posterior) of fishes and Petromyzontids (cf. STENSIÖ 1922, p. 172; 1925 a, p. 21; 1925 b, p. 102; GROSSER 1907, fig. 4; O'DONOGHUE 1914, p. 442; POLLARD 1892, pl. 29, fig. 23; ALLEN 1905, p. 87—89; REX 1891, pls. 15, 16; CORI 1906, pp. 50—51; HATTA 1922, pp. 180—182 and the chapter on the Petromyzontids below in the present work).

The branch (IX) from the vagus canal, following next ventrally to the one just described for the vena cerebralis posterior, is, in the specimen used for section series B, very well separated from the most ventral branch, while, on the contrary, in the specimen used for section series A it is less distinctly bounded off from that branch. It goes laterally and somewhat ventrally, opening with its external orifice on the posterior surface of the otic region dorsally to but behind the postbranchial wall, and thus behind the oralo-branchial chamber (text-figs. 13, 14). From its external orifice a groove leads, at least in certain specimens (text-fig. 14), for a certain distance laterally, and perhaps even slightly dorsally, on the posterior surface on the otic region, finally deepening and passing over into a canal, IX *p*, (text-figs. 13, 14) which penetrates in an antero-lateral direction to the labyrinth cavity (IX *p*, text-figs. 18 A, C, E; 24, 26; cf. pl. 25) or, more exactly, to the vestibular division (*vest*) of that cavity. Since, as we shall see, the glossopharyngeus roots had no independent canal for their passage from the cavum cerebrale cranii, they must obviously have left this cavity associated with the vagus roots. And when this is the case, we are led to the conclusion that is was the glossopharyngeus roots that emerged through the second branch from above (IX) — the one here in question — of the vagus canal. Hence this branch may be called the glossopharyngeus branch of the vagus canal.

The glossopharyngeus roots probably first became ganglionic after their exit from the glossopharyngeus canal; and the glossopharyngeus ganglionic complex thus lay extracranially, posteriorly to the otic region and the oralo-branchial chamber. The n. glossopharyngeus, which arose from the ganglionic complex, passed first laterally through a groove on the posterior surface of the otic region and then antero-laterally to the vestibular division of the labyrinth cavity through the canal IX *p*.

It may here be noticed that the glossopharyngeus branch of the vagus canal, in addition to the root or the roots of the n. glossopharyngeus, perhaps gave passage also to the post-otic lateralis nerve-fibres.

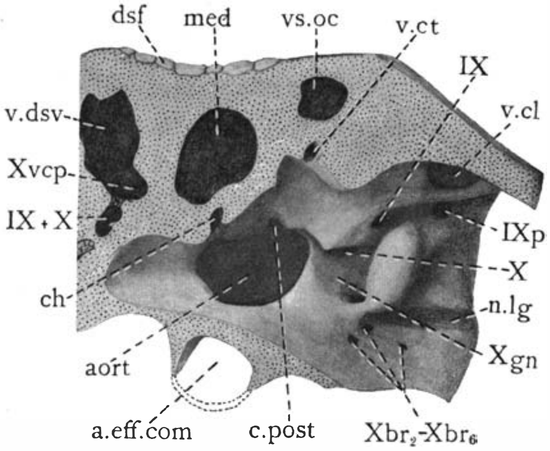
Finally the most ventral branch (X) of the vagus canal of *C. hoeli* always takes a course more ventrally than the former branch and opens therefore often somewhat medially and ventrally to that, posteriorly to the most dorsal part of the postbranchial wall and on the right side close laterally to the aortal groove (text-figs. 13, 14), which, even as far forward as this, still does not lie exactly in the median line. It is quite obvious that this branch transmitted the roots of the n. vagus proper and perhaps in addition the most posterior postotic lateralis root or roots; and on account of this it may be referred to as the vagus branch proper of the vagus canal.

The external orifice of the vagus branch proper of the vagus canal leads at least in certain specimens to a rather pronounced fossa *Xgn* (text-fig. 14) on the posterior surface of the postbranchial wall. And it may be especially mentioned that in some cases this fossa was entirely open backwards (text-fig. 14), while in other cases it seems to have been more or less bridged over by bone on the posterior side, so that it was thus transformed into an imperfectly closed chamber (text-fig. 34).

From the fossa *Xgn* more or less close to the distal opening of the vagus branch proper of the vagus canal a rather fine canal X_{br_1}, issues forwards into the basal part of the otic region (text-fig. 13, 28, 33, 34; section series A, nos. 62—68; section series C, nos. 79—86; section series E, nos. 7—12; section series F, nos. 1—3; cf. pls. 28, 52) within which is continues forwards, finally opening anteriorly to the postbranchial wall in the roof of the oralo-branchial chamber. As we shall see from the account given below of the otic region and the visceral endoskeleton we are here, in the canal X_{br_1}, concerned with the canal for the first branchial branch of the n. vagus, which thus, at least in certain specimens of *C. hoeli*, arose already very close to or within the distal of the vagus branch proper (X) of the vagus canal.

As the first branchial branch of the n. vagus thus, at least in certain cases, arose already in the external parts of the vagus canal proper, it is highly probably that the roots of the n. vagus began to become ganglionic even before leaving that canal. The chief part of their ganglionic complex, however, must have been situated in the fossa *Xgn*, or at a corresponding place on the posterior surface of the postbranchial wall if the said fossa was not present in all specimens.

After its origin from the ganglionic complex, the n. vagus must have passed downwards and postero-laterally behind the postbranchial wall for a short distance. Probably already when leaving the ganglionic complex it divided into two or three trunks, which soon diverged slightly from each other and perforated the upper medial part of the postbranchial wall independently of each other and entered the postero-dorso-medial part of the oralo-branchial chamber behind the auditory prominence of their side. The canals for the branchial trunks in question of the n. vagus are those which in the figures are denoted by the letters X_{br} or X_{br_2}—X_{br_6} (text-figs. 14, 33, 34, 39, 40; and section



Text-fi. 14. *Cephalaspis hoeli.* Restoration showing the conditions at the glossopharyngeus and vagus exits of the right side. The chief posterior part of the occipital region rcmoved. The restoration was made after section series B. Section surfaces dotted. The dotting also denoting the extension of the cartilage in the interior of the endocranium at the section plane. Magnification approximately 8/1. *a. eff com*, canal for the arteria branchialis efferens communis, a vessel formed by the confluence of the efferent branchial arteries 4—6; *aort*, canal for the aorta; *ch*, groove for the notochord; *c. post* canal for the posterior encephalic artery; *dsf*, dorsal electric field; *med*, division of the cavum cerebrale cranii for the medulla oblongata; *n. lg*, groove perhaps for the n. lineae lateralis; *v. cl*, canal for the vena capitis lateralis (posterior opening); *v. ct*, canal probably for a parietal vein which was in communication with the occipital vein sinus; *v. dsv*, canal for the otical vein (from the dorsal electric field and the labyrinth. The ductus endolymphaticus may perhaps also have reached backwards through this canal); *vs. oc*, occipital vein sinus; IX, branch of the vagus canal for the roots of the n. glossopharyngeus; IX_p, canal for the n. glossopharyngeus through the posterior part of the otic region; X, branch of the vagus canal for the vagus roots; X_{br2}—X_{br6}, canals through the postbranchial wall for branchial branches of the n. vagus; *Xgn*, pit probably for the vagus ganglionic complex; *Xvcp*, branch of the vagus canal for the v. cerebralis posterior.

series B, nos. 8—14; section series C, nos. 77—80; section series E, nos. 7—10; section series F, nos. 1—19).

A groove (*n. lg*, text-fig. 14, 34; section series B, nos. 14—18; section series F, nos. 1—5), which, at least in certain specimens, begins laterally to the ventral end of the fossa *Xgn*, and which leads laterally on the upper part of the posterior surface of the postbranchial wall, immediately ventrally to the otic region, was perhaps caused by the n. lineae lateralis, which must have passed out to the lateral line of its side in a rather straight lateral direction.

Finally, attention should here be called to the fact that, in the specimen of *C. hoeli* used for section series B (nos. 14—18), two fine canals (IX*l*, X*l*) issue from the vagus canal to the vestibular division of the labyrinth cavity. More exactly, one of these fine canals (IX*l*) passes off from the glossopharyngeus branch, while the other (X*l*) goes out from the vagus branch of the vagus canal; and both the fine canals in question unite with each other before they reach the vestibular division of labyrinth cavity. What functions the two canals may have had cannot be positively ascertained; but it seems rather likely that they might have been traversed by general cutaneous branches from the n. glossopharyngeus and the n. vagus to the dorsal side of the cephalic shield above and just posteriorly to the otic region. It is also not excluded that certain of the lateralis fibres to the lateral line organs above and behind the otic region may have accompanied the possible general cutaneous fibres this way to their respective parts of the lateral line system on the dorsal side of the cephalic shield.

In the specimen of *Kiaeraspis* in which the vagus canal was studied (text-figs. 4, 20—22, 27, 28, 36; section series D, nos. 1—20), its glossopharyngeal branch and its vagus branch proper are not separated from each other but form in their entire extent a single wide branch, and in addition no groove seems to lead from the external opening of that common glossopharyngeus-vagus branch to the place at which the n. glossopharyngeus entered its forward-running canal, IX *p*, in the otic region. Otherwise the conditions seem to agree with those in *C. hoeli*, and it may be especially mentioned that there is an independent canal (X_{br_1}, pl. 52) for the first branchial branch of the n. vagus. The different parts of the vagus canal of the specimen in question of *Kiaeraspis* are well shown in the figures quoted.

In several of the Cephalaspids figured in the plates (pl. 23, fig. 3; pls. 25, 26, 28, 44, 45, 49, 52, 54 and 55) various parts of the vagus canal and its branches are to be seen, but none of these Cephalaspids displays it completely.

Close medially to the internal opening of the vagus canal there issue from the cavum cerebrale cranii in all forms investigated two comparatively fine canals, one of which (*c. post*, text-figs. 16, 21, 24, 28; section series A, nos. 51—54; Ser. B, nos. 11—14; Ser. C, nos. 11, 12, 13, 36—45, Ser. D, 4—9; pl. 23, fig. 3; pl. 44) goes downwards through the floor, and the other (*dx*, text-figs. 15, 17, 18—20, 22, 23, 26; section series A, 49—53; series B, 17, 18; ser. C, 1—5, 27—31; Ser. D, 13—24) goes upwards through the roof. The former of these canals, which is very short, continues (*c. post*) down to the aortal groove or, more correctly, to the aortal canal, since the aortal groove just at this place is bridged over ventrally by the post-branchial wall. As the aortal canal here still lies somewhat asymmetrically on the right side of the median line the right canal is shorter than the left one. In addition to this the right canal — which, as a rule, seems to lie more forward than the left one — is often considerably wider than that. From its course and its asymmetrical development it seems to be beyond question that this canal transmitted a dorsal branch from the pars cephalica aortae, that is to say, an arterial branch which entered the occipital region of the neurocranium, and which may therefore be called the occipital encephalic artery. This artery probably corresponded to the 4th "Gefäßbindeglied" found by HATTA (1922, pp. 136—148) in the larvae of *Petromyzon* and thus probably to the fourth parietal artery counted from in front (cf. the chapter on the Cyclostomes in this work).

The other canal (*dx*), which is somewhat longer than the one just described, issues almost opposite — or at least not much anteriorly or posteriorly to that — and at least in several cases, it is on the right side situated more forwards than on the left side. It goes antero-dorso-laterally to a big vein canal (*v. dsv*), which will be described more in detail below. What function it had is not easy to decide with full certainty; but from what we shall find below it may have transmitted a dorsal branch from the occipital encephalic artery and a nerve branch from the glossopharyngeus-vagus complex to the dorsal electric field or either of these structures. Its function will be further discussed in another connection below.

Somewhat behind the vagus canal two paired canals (nd_1, and nv_1, text-figs. 15—17, 20—28; section series A, nos. 14—33; section series C nos. 1—8; section series D, nos. 20, 26—33; pl. 18; pl. 19, fig. 1; pl. 23, fig. 3; pl. 44; pl. 53, fig. 1) issue from the occipital division of the cavum cerebrale. More closely defined, these canals leave the occipital division of the cavum cerebrale just at or close behind the transition between its anterior widened and its posterior narrow tube-like parts, and those of the right side are found somewhat in front of those of the left side.

One of these canals, lettered nv_1 in the figures, goes out on the lateral side more or less near the bottom of the cavum cerebrale. This canal, which mostly is very fine and difficult to observe, perforates the laterall wall of the cavum cerebrale in an outward and slightly postero-ventral direction; and since the lateral cranial wall at this place — we are here concerned with the neural ridge — is thin it is rather short. There cannot be the slightest doubt that it transmitted the first spino-occipital nerve or at least the ventral root of this spino-occipital nerve. And in addition it is very probable that it was traversed by a myelonal artery (STERZI 1907, pp. 41—43; ALLEN 1905, p. 74).

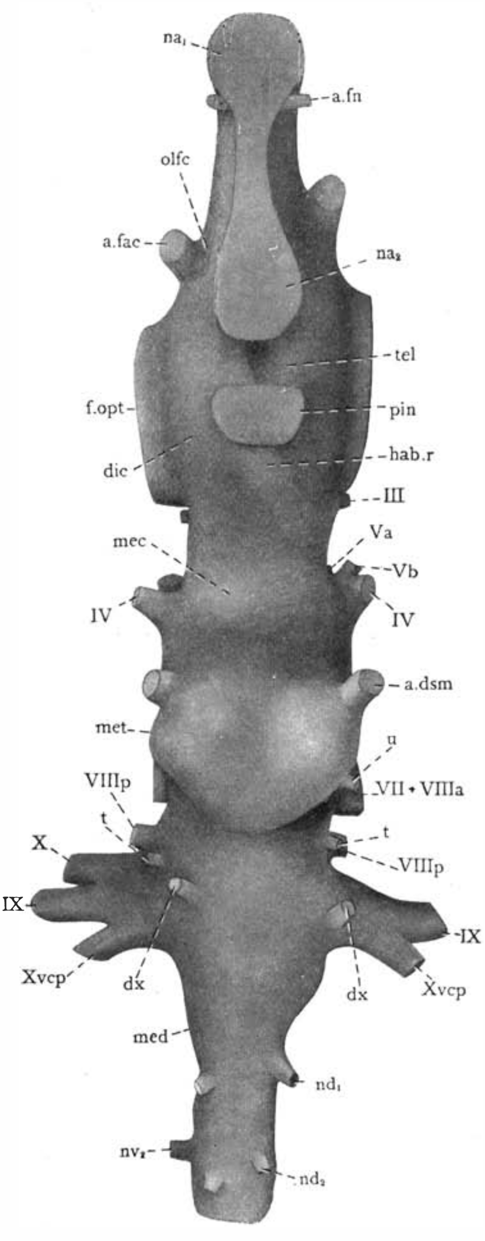
The other of the two canals, lettered nd_1 in the figures, is wider than the one just described; and it always issues from the cavum cerebrale dorsally to and somewhat behind the other one. It goes postero-latero-dorsally in the lateral thin but broad portion of the occipital region that is situated laterally to the neural ridge. Having passed for a rather considerable distance postero-latero-dorsally it may either join (*Kiaeraspis*) or, by means of a short wide branch, anastomoze with the postero-dorso-medial corner of the occipital vein sinus (*vs. oc*) to be described below. From that corner of the occipital vein sinus a short wide branch (d_1, text-fig. 23) goes upward and somewhat medially, opening in the very lateral border of (cf. section series A, nos. 23—27 and pl. 32, fig. 2) or — as in *Thyestes verrucosus* — slightly postero-laterally to the dorsal electric field. In the specimen of *Cephalaspis hoeli* used for section series A it is clearly seen that the canal nd_1, after having joined or anastomozed with the posterior end of the occipital vein sinus, continues postero-laterally for a certain distance; but how far it really went in that direction and how it might have been in its very posterior part cannot be ascertained there. Close antero-laterally to it there is in the same specimen of *C. hoeli* a rather narrow canal (nd_1l), which leaves the posterior end of the medial corner of the occipital vein sinus and goes laterally and somewhet backward until it reaches and opens into the canal (*v. ol*) for the lateral occipital vein. The canal nd_1l, therefore, was probably a vein canal.

In the specimen of *Hoelaspis* figured in pl. 44 the canal which is seen issuing from the occipital division of the cavum cerebrale next behind the vagus canal has such a position and course that probably it is identical with the canal nd_1. This is all the more probable since, as far as I could see, there is no other canal with such a high position between it and the vagus canal. It is very remarkable that this canal in *Hoelaspis* opens on the lower side of the occipital region not far dorso-laterally to the neural ridge, and that it seems to have no communication with the occipital vein sinus. The latter condition may, however, only be apparent and due to the state of preservation.

The canal nd_1 must obviously have given passage to the first myelonal vein (vertebro-medullary vein, STERZI 1907, pp. 41—43; ALLEN 1905, pp. 88). But since the myelonal veins — at least often in lower vertebrates — accompany the dorsal roots of the spinal nerves, it seems very likely that the canal nd_1 was traversed not only by the first myelonal vein but also by the dorsal root of the first spino-occipital nerve. And if this is true, the canal nv_1 transmitted of course only the ventral root of this spino-occipital nerve. Now since the two canals nd_1 and nv_1 diverge much from each other during their course outwards, the dorsal and ventral roots of the first spino-occipital nerve could not have united with each other as normally in vertebrates but must have been entirely separated from each other, as in *Amphioxus* and the Petromyzontids.

If, on the contrary, it would appear that the canal nd_1 is merely a canal for myelonal vein, the canal nv_1 must, of course, have transmitted the entire first spino-occipital nerve whether that nerve was represented only by the ventral root or had both its roots; but it seems hardly likely that it was so.

A rather short distance behind the two canals nd_1 and nv_1 two additional, paired canals — lettered in the figures nd_2 and nv_2 respectively and situated in relation to each other in a corresponding way as nd_1 and nv_1 — issue from the cavum cerebrale cranii (text-figs. 15—17, 23—26; section series A, nos. 2—20; section series C, nos. 9—15, 20—46;



Text-fig. 15. *Cephalaspis hoeli.* Cast of the cavum cerebrali cranii in dorsal view. After a model in wax made after section series A. Magnification approximately $^{17}/_{1}$.

a. dsm, canal for the arteria superficialis postorbitalis; *a. fac*, canal for the arteria facialis; *a. fn*, canal for a branch from the facial artery to the external opening of the hypophyseal sac; *dic*, division of the cavum cerebrale for the diencephalon; *dx*, canal for an artery or a nerve to the posterior part of the dorsal electric field or for both an artery and a nerve; *f. opt*, optic fenestra; *hab. r*, bulge for the habenular ganglia. Note the asymmetric position, indicating that the right ganglion was more strongly developed than the left one; *mec*, division of the cavum cerebrale for the mesencephalon; *med*, division of the cavum cerebrale cranii for the medulla oblongata; *met*, division of the cavum cerebrale cranii for the metencephalon; na_1, external opening of the hypophysial sac; na_2, nasal opening proper; nd_1, canal for the first myelonal vein and probably also for the dorsal root of the first spino-occipital nerve 1; nd_2, canal for the myelonal vein 2 and probably also for the dorsal root of spino-occipital nerve 2; nv_1, canal for the myelonal artery 1 and probably for the ventral root of the spino-occipital nerve 1; nv_2, canal for the myelonal artery 2 and probably for the ventral root of spino-occipital nerve 2; *olf. c*, olfactory capsule: *pin*, pineal opening; *tel*, division of the cavum cerebrale cranii for the telencephalon; *t*, *u*, canals probably for vessels; *III*, canal for the n. oculomotorius; *IV*, canal for the n. trochlearis; *Va*, *Vb*, canals for the roots of the n. profundus; *VII+VIIIa*, canal for the n. facialis, for the prootic lateralis fibres, for the electric fibres and for the anterior branch of the n. acusticus; *VIIIp*, canal for the posterior branch of the n. acusticus; *IX*, branch of the vagus canal for the glossopharyngeus roots; *X*, branch of the vagus canal for the vagus roots; *Xvcp*, branch of the vagus canal for the vena cerebralis posterior.

pls. 23, fig. 3; *spi*, pl. 53, fig. 1). These two canals of the right side always leave the cavum cerebrale somewhat anteriorly to their fellows of the left side, so that it is clearly seen here that the canals of both sides alternated with each other; and in this connection attention may be called to the fact that the canals nd_1 and nv_1 of the right side also went out from the cavum cerebrale cranii in front of their fellows of the left side, though less far than the canals nd_2 and nv_2.

The canal nv_2 sometimes leaves the cavum cerebrale cranii at about the same level as the canal nv_1, sometimes a little higher up than that. In addition it is often wider than that. It goes in a postero-lateral direction through the cranial wall (the lateral wall of the neural ridge), opening with an external opening which sometimes may be somewhat widened. Since in the *Cephalaspis*-species and in the other forms with a short occipital region it is situated just at the transition to the most postero-ventral part of the occipital region, that was not lined with perichondral bone and thus entirely cartilagenous it is often badly or imperfectly preserved and indistinct in the fossils. It must obviously have had a similar function as the canal nv_1 and accordingly it transmitted besides the second myelonal artery either the entire second spino-occipital nerve or the ventral root of that nerve.

The canal nd_2 could be studied in detail only in the specimen of *C. hoeli* used for the section series A. Proximal parts of it, however, are seen in a second specimen of that species (pl. 23, fig. 3), so that there can be no doubt that it is a constant structure. It issues from the cavum cerebrale far dorsally to nv_2 and takes a postero-dorso-lateral course, soon arriving up close beneath the exoskeleton, immediately laterally to the hindmost part of the dorsal electric field, to which it gives off a fine branch (d_2, text-figs. 23, 25; section series A, no. 14; section series C, nos. 26—30). Posteriorly to that branch it divides into a medial and a lateral branch. The medial of these branches is in communication with its fellow of the opposite side above the cavum cerebrale cranii and the lateral one with the canal for the lateral occipital vein (*v. lo*), to be described below.

From its course and its mode of branching it is quite clear that the canal nd_2 in several respects agrees with the canal nd_1; and, therefore, it cannot be doubted that it is a serial homologue of that. In fact, if the canal nd_1 transmitted not only the myelonal vein 1 but also the dorsal root of the spino-occipital nerve 1, the canal nd_2 must have given passage not only to the myelonal vein 2 but also to the dorsal root of the spino-occipital nerve 2.

In the *Cephalaspis*-species, and in other forms with an occipital region of a short or average length, there was perhaps a third spino-occipital nerve in the most posterior cartilaginous part of the occipital region. In forms with a long occipital region (*Kieaeraspis*) the spino-occipital nerves were certainly rather numerous perhaps, even as many as 9 or 10.

The study of the nerve canals which occur in the occipital region has thus given the following results:

1. The roots of the n. glossopharyngeus left the cavum cerebrale cranii through the vagus canal, together with the vagus roots. And both the glossopharyngeus and vagus roots emerged from the vagus canal posteriorly to the postbranchial wall and had at least the chief parts of their ganglionic complexes situated extracranially posteriorly to the postbranchial wall. The n. vagus had to pierce the postbranchial wall in order to reach the gills in the oralo-branchial chamber.
2. The vena cerebralis posterior traversed the most dorsal part of the vagus canal and emptied into the occipital vein sinus.
3. In the *Cephalaspis*-species, and in other Cephalaspids with a short occipital region there are at least, two but not more than three, spino-occipital nerves. In *Kiaeraspis* the spino-occipital nerves were probably still more numerous.
4. The nerves of both sides of the occipital region, both the n. vagus and the spino-occipital nerves of both sides, were not situated opposite each other but alternated with each other, as the spinal nerves do in *Amphioxus* and recent Cyclostomes.
5. There are certain facts which indicate that the dorsal and ventral roots of the spino-occipital nerves probably did not unite, but went separate, as the spinal nerves do in *Amphioxus* and Petromyzontids.

Now when we are able to establish that the nerves of the occipital region both alternated with each other on both sides and in addition that probably the dorsal and ventral roots of each spino-occipital nerve did not unite with each other, we are justified in concluding that similar conditions prevailed, also so far as the spinal nerves are concerned, and thus that these alternated with each other and had their ventral and dorsal roots entirely separate.

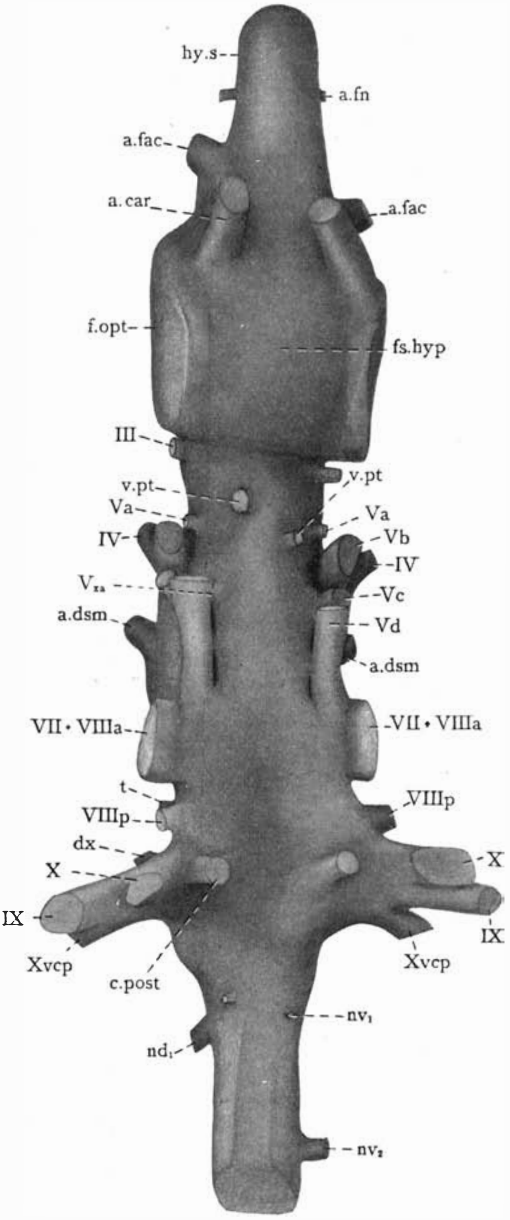
After this description of the nerve-canals we turn to the vein canals of the region.

In the most anterior part of the region and in the hindmost part of the otic region, immediately behind the posterior semicircular canal, we find a big paired vein sinus, the occipital vein sinus, which has already been referred to above. This vein sinus (*vs. oc*, text-figs. 14, 23—28; section series A, nos. 27—46; section series B, nos. 2—16; section series C, nos. 49—73; section series D, nos. 1—40; pl. 19, fig. 1; pls. 25, 26, 29, 49, 54, 55) is more or less distinctly tetraedral in shape, and has always its postero-dorso-medial corner produced backwards and, at least in *Cephalaspis hoeli*, anastomosing with the canal nd_1. From the dorsal side of that produced corner there issues, as already mentioned, the short rather wide canal d_1 (text-fig. 23; section series A, nos. 23—27; pl. 32, fig. 2) in a dorsal direction. And while in the *Cephalaspis*-species and other forms with a long dorsal electric field the said canal d_1 leads to, and opens on, the very lateral border of the dorsal electric field it ascends, on the contrary, in *Thyestes verrucosus*, and probably also in other forms with a short dorsal electric field, up to the dorsal surface of the exoskeleton slightly postero-laterally to the dorsal electric field. And attention may be called to the fact that in *Tremataspis* too the canal has its dorsal orifice postero-laterally to the dorsal electric field, as in *Thyestes verrucosus*.

If we knew the canal d_1 only in the *Cephalaspis*-species it would of course be considered simply as a vein canal, which transmitted a tributary to the occipital vein sinus. The conditions in *Thyestes verrucosus*, however, seem to indicate that this cannot have been the case, for we cannot imagine that in these forms such a big vein as it would be the question of here arose and passed so superficially as to enter and traverse the canal d_1. As we shall see from the account given below of the otic region and the labyrinth cavity, it is possible that the ductus endolymphaticus might have persisted and reached up to the epidermis through the said canal. But in the *Cephalaspis*-species it seems not inconceivable that in addition a vein from the dorsal electric field went down to the occipital vein sinus this way.

Besides the canal d_1, there were several other canals which opened into the occipital vein sinus, and which quite certainly were traversed by tributaries to that sinus. The most important ones of these canals are as follows: the canal for the v. cerebralis posterior, a canal from the otic region, a number of dorsal and lateral canals, usually rather narrow, from the subaponeurotic vascular plexus, and finally, at least in certain *Cephalaspis*-species, a canal from the postero-lateral parts of the occipital region.

The first-mentioned one of these canals, the canal for the v. cerebralis posterior (X*vcp*, text-figs. 15—17, 20—24, 26—28; section series A, nos. 44—48; section series B, nos. 2—14; section series C, no. 41—55; section series D, nos. 8—20; pls. 25, 26, 44, 45, 49, 55) forms, as we have seen, the most dorsal branch of the distal part of the vagus canal, and consequently the v. cerebralis posterior, though it was strikingly wide, had a quite normal course. From the posterior side of the canal for the v. cerebralis posterior there issues a short rather wide canal lettered in the figures *v. ct* (text-figs. 14, 24, 26; section series A, nos. 40—43; section series B, nos. 2—7; section series D, nos. 15—24; pl. 26), which goes backwards and opens on the lower side of the occipital region somewhat postero-dorso-medially to the neural branch or neural branches of the vagus canal and rather close to the neural ridge. It is worthy of



Text-fig. 16. *Cephalaspis hoeli.* Cast of the cavum cerebrale cranii from the ventral side. After a model in wax made from section series A. Magnification approximately $^{17}/_{1}$.

a. car, canal for the carotid artery; *a. dsm*, canal for the postorbital superficial artery; *a. fac*, canal for the arteria facialis; *a. fn*, canal for a branch from the facial artery to the external opening of hypophysial sac; *c. post*, canal for the posterior encephalic artery; *dx*, canal for an artery or a nerve to the posterior part of the dorsal electric field, or for both an artery and a nerve; *f. opt*, optic fenestra; *fs. hyp*, fossa hypophyseos; *hy. s*, division of the ethmoidal cavity for the hypophysial sac; nd_1, canal for the first myelonal vein and probably also for the dorsal root of the first spino-occipital nerve; nv_1, canal for the myelonal artery 1 and probably also for the ventral root of spino-occipital nerve 1; nv_2, canal for the myelonal artery 2 and probably also for the ventral root of spino-occipital nerve 2; *t*, canal probably for a vessel; *v. pt*, canal probably for the pituitary vein; III, canal for the n. occulomotorius; IV, canal for the n. trochlearis; V*a*, canal probably for the viscero-motor root of the n. profundus; V*b*, canal for the general cutaneous root of the n. profundus; V*c*, V*d*, canals for the roots of the n. trigeminus proper; V*c*, for the general cutaneous root; V*d*, probably for the viscero-motor root and the n. abducens; V*xa*, canal perhaps for the n. abducens; VII+VIII *a*, canal for the n. facialis, for the electric nerve fibres, for the prootic lateralis fibres, and for the anterior branch of the n. acusticus; VIII *p*, canal for the posterior branch of the n. acusticus; IX, branch of the vagus canal for the glossopharyngeus roots; X, branch of the vagus canal for the vagus roots; X*vcp*, branch of the vagus canal for the vena cerebralis posterior.

notice, however, that the external opening of this canal of the right side, since it is situated laterally to the aortal groove, lies somewhat farther from the neural ridge than the one of the corresponding canal of the left side. In *Kiaeraspis* the canal *v. ct*, of each side is connected by means of a dorsal rather fin branch (*v.* ct_1 section series D, nos. 20—28), with the dorso-medial corner of the occipital vein sinus. According to their course and position the canals *v. ct* and *v.* ct_1 seem to have been traversed by branches of one of the anterior parietal veins (cf. HATTA 1922, pp. 182—185; cf. also text-fig. 99 in the present work).

The canal (*v. dsv*, text-figs. 14, 18, 19, 23, 26, 27; section series A, nos. 47—49; section series B, nos. 6—18; section series C. nos. 31—53; section series D, nos. 24—40; pl. 13, fig. 3) which from the otic region leads to the occipital vein sinus is generally very wide. It issues, as will be described in detail below in connection with the account of the labyrinth cavity, from the dorso-medial parts of the labyrinth cavity or from a canal which from this cavity goes to the dorsal electric field; and it passes off in a postero-lateral direction to the antero-dorso-medial part of the occipital vein sinus. It seems to have transmitted a vein, which, as far as can be judged, drained a middle part of the dorsal electric field and at least certain dorsal parts of the labyrinth, and on account of this, it may be termed the canal for the otical vein. Besides the otical vein this canal may possibly also, as we shall see, have lodged the ductus endolymphaticus.

The fine canals which, from the subaponeurotic vascular plexus pass to the occipital vein sinus are well shown in the text-figs. 23—27, as well as in several of the section series (section series A, nos. 35—46; section series B, nos. 1—16; series C, nos. 53—57; section series D, nos. 20—43). As is clearly seen from the figures quoted, they open mostly on the dorsal and lateral sides of the occipital vein sinus. At least in *C. hoeli* the biggest of them are distinctly paired.

Finally, the canal (*v. ol*, text-figs. 23—26; section series A, nos. 2—33; section series C, nos. 63—68), which from the posterior lateral parts of the occipital region goes forward to the occipital vein sinus is well known only on one side in a specimen of *Cephalaspis hoeli*, the specimen used for section series A. Except most posteriorly it is situated in the lateral portions of the thin lateral parts of the region. Into it open several canals both on the lateral and on the medial side, the latter being branches of, or else branches which indirectly communicate, with the canals nd_1 and nd_2. It lodged a vein which must have drained the postero-lateral and most posterior parts of the occipital region of the endocranium as well as the exoskeleton above these parts. According to its position, this vein may be called the lateral occipital vein and the canal for it the lateral occipital vein canal.

In *Kiaeraspis* no canal could be observed corresponding to that of *Cephalaspis hoeli* described here as the canal for the lateral occipital vein. But since the conditions in *Kiaeraspis* are otherwise very similar to those in *C. hoeli*, it seems rather strange if the lateral occipital vein should not have existed in it too. And at present, therefore, I am inclined to think that the absence of the canal in question in *Kiaeraspis* is only apparent and due to an unfavorable state of preservation in the single specimen used for sections (section series D).

As is evident from the description now given of its tributaries the occipital vein sinus received almost the entire quantity of venous blood of the occipital region and in addition a considerable quantity of venous blood from the otic region. With its ventro-lateral more or less extended and narrow corner it opens into the very posterior part of the canal for the vena capitis lateralis. And it is thus quite clear that it emptied its blood into the vena capitis lateralis. (Cf. further the otic region and the chapter on the vascular system).

Besides the canals now described, we find in the occipital region two further canals which perhaps are not constant but which nevertheless deserve to be taken into consideration. One of these canals (*vy*, text-fig. 27; section series D, nos. 24—35) is found in the specimen used for sections of *Kiaeraspis.* It issues from the left side of the cavum cerebrale cranii slightly postero-dorsally to the vagus canal and goes postero-dorso-laterally, medially to the left occipital vein sinus. As it is very fine it was difficult to trace on the sections, nor was it possible to observe how it ended dorsally, whether it opened into the occipital vein sinus or whether it had no relations to that. What its function might have been cannot be decided with certainty, but it seems not improbable that it transmitted a vein. The other canal to be described here has been found only in the specimen of *C. hoeli* used for section series B. It (section series B, no. 10) is a fine one which lies in the angle between the branch of the vagus canal for the v. cerebralis posterior and the branch of the same canal for the glossopharyngeus roots. As it could not be traced either to its origin or to its termination, it is so far impossible to decide what its function might have been.

Otic region. — The otic region (text-figs. 2, 3, 4, 5, 7, 8, 13, 14) is not well bounded externally either from the adjacent regions or from the parts of the visceral endoskeleton with which it is continuous laterally. Probably owing to the position of the orbits far dorso-medially its dorso-lateral parts hardly extend so far forwards as its ventro-medial ones. In addition attention must here be called to the fact that certain of the trigeminus roots left the cavum cerebrale cranii very far behind the others, in reality in the otic region, and that on account of this it often may be very difficult to decide exactly at what place the transition between that region and the orbitotemporal region takes place.

The otic region, which always is shorter than the occipital region and approximately of the same length as the orbitotemperal region, is very broad, its breadth usually being about three times as great as the length. Its height, which is greater than that of the occipital region, is probably subject to a certain variation, but seems, as a rule, to be almost one third of the breadth and thus not so very much less that the length. Being continuous laterally with the visceral endoskeleton the region has of course no free lateral borders. Like the occipital region it presents a dorsal and a ventral surface but has in addition also anterior (orbital) and posterior surfaces, the latter two of which are paired.

The dorsal surface as a whole is convex (text-figs. 2 B; 3, 5; section series A, nos. 44—99; section series B, nos. 1—38) with a wide median fossa, which is occupied by the dorsal electric field.

The ventral surface (text-figs, 2, 3, 4, 13, 33, 36, 41; pls. 52, 54, 56) which is lined by the external perichondral bone-layer and which forms part of the upper surface of the oralo-branchial chamber, is slightly concave in transversal direction. It is bounded anteriorly by the transverse orbito-otical groove (*orb. ot. gr*, text-figs. 4, 13) and posteriorly by the postbranchial wall (*p. brw*). While that wall most medially descends from the endocranium approximately at the transition to the occipital region we find it, on the contrary, more laterally descending instead from the posterior parts of the bottom of the otic capsules. And owing to this the posterior surface of the otic capsule of each side, which is here called the posterior surface of the region, is freely exposed behind the postbranchial wall. On the ventral surface we find, as we have already had occasion to point out (p. 45 above), the median, longitudinal aortal ridge (*r. aort*) with the aortal groove (*aort. gr*), the latter of which in its posterior part, belonging to the region, is bridged over on the ventral side and thus transformed into a canal. As we have also found, there is on each lateral side of the aortal ridge a distinct bulge, the otical prominence (*pr. au*), caused by the auditory organ. In certain forms, such as *Hoelaspis* (pl. 44) and *Kiaeraspis* (*ibr*$_4$, text-figs. 4, 36; pls. 51, 52), the fourth interbranchial ridge always continues across the anterior part of the otical prominence close behind the orbito-otical groove as far dorsomedially as to the aortal ridge.

The anterior surface, which is paired and rather small, forms part of the boundary of the orbit and is lined by the orbital perichondral bone-layer. In accordance with the shape of the orbit it is somewhat concave in both dorsi-ventral and transversal directions and it passes over into the ventral and medial surfaces of the orbit.

Finally, as was mentioned above, the posterior surface, which, like the anterior one, is small and paired, lies entirely behind the postbranchial wall (text-figs. 13, 14). It faces postero-ventrally and sometimes also slightly laterally and is often as a whole slightly concave in both transversal and dorsi-ventral directions. Medially and dorsally it is continuous with the lower surface of the occipital region and ventrally it passes over into the posterior surface of the postbranchial wall.

The division of the cavum cerebrale cranii falling within the region in question (text-figs. 2, 15—17, 20—28; section series A, nos. 56—99; section series B, nos. 1—38; section series C, 1—40; section series D, nos. 2—33; pl. 13, fig. 3, pls. 14, 18; pl. 19, fig. 1; pls. 26, 45, 48, 49, 55, 59) lies with the middle and posterior parts of its bottom somewhat lower than the division enclosed in the occipital region. Most posteriorly it is in certain forms somewhat narrower and perhaps even slightly lower than the most anterior part of the last-mentioned division. But if we proceed forwards, we find that it very soon begins to get higher and that it already behind the middle of the region is almost twice as high as most posteriorly, whereas its breadth has increased rather slightly or remains rather uncharged. More anteriorly in the anterior half of the region it gets lower again and at the same time also somewhat narrower. Laterally it is bounded by a thick wall from the labyrinth cavity of each side, a wall which is perforated solely by the canals for vessels and nerves, that pass out from the cavum cerebrale.

For the further description we may consider the otic region to be composed of a ventral wall, a dorsal wall and a paired lateral wall.

The first-mentioned of these walls, the ventral wall (text-figs. 2, 4, 33, 36, 41; section series A, B, C, D, F; pls. 14, 15, 44, 45, 48, 49, 50, 52, 55), forms anteriorly on its dorsal side a rather high pronounced dorsum sellae (*d. sell*, section series A, no. 99; section series C, nos. 1—30; section series D, nos. 1—7) and is there throughout its breadth rather thick. More posteriorly, on the contrary, its median part which separates the cavum cerebrale from the aortal groove is rather thin. Posteriorly and laterally it is continuous with the visceral endoskeleton. More exactly, it passes over posteriorly into the postbranchial wall and laterally into the lateral part of its side of the visceral endoskeleton. It is pierced in the median part above the aortal groove by a fine canal (*ch*), which forms the direct anterior continuation of the notochordal groove of the occipital region and which therefore must have lodged the notochord. As is seen particularly from section series A (nos. 56—99), this canal, which is lined by a perichondral bone-layer of its own, is very fine. Most caudally where at least in the specimens used for section series A (nos. 56—60) and B (nos. 8—18) it is higher than it is broad, it lies approximately in the middle of the height (thickness) of the ventral wall. Further forwards it soon descends to the ventral surface of the ventral wall, decreasing in diameter and getting first a rather circular, then a dorso-ventrally flattened shape (section series A, nos. 61—95; section series B, nos. 19—29). It should also be mentioned that during this part of its course it lies almost in the very dorsal surface of the aortal groove, and that its ventral boundary is formed only by a very thin layer of perichondral bone. It retains this ventral position until as far forward as beneath the dorsum sellae, then most anteriorly it curves upwards into the dorsum sellae, ending into the most antero-dorsal part of that (section series A, nos. 97—99; section series B, nos. 30, 31). We are thus able to establish that the notochord extended forward through the entire occipital and otic regions, though it was very delicate. The notochordal canal is to be seen not only in the specimens quoted but also in that used for section series C (nos. 18—20) and in several others (pl. 23, fig. 3; pl. 46, fig. 1; pls. 49, 52, 55.

The postero-lateral part of the ventral wall is constantly pierced by a paired canal, X_{br_1}, for the most anterior branchial branch of the n. vagus. This canal, which as we have seen issues from the fossa X*gn* goes antero-laterally and slightly ventrally beneath the labyrinth cavity to the oralo-branchial chamber, opening there either as in most *Cephalaspis*-species close posteriorly to the otic prominence or, as in certain *Cephalaspis*-species and *Kiaeraspis*, somewhat postero-laterally to that prominence. The canal in question is more or less well shown in certain of the text-figures and plates (text-figs. 4, 13, 33, 34; section series A, nos. 62—68; section series C, nos. 79—86; section series E, nos. 7-—12; section series F, nos. 1—3; pls. 28, 52).

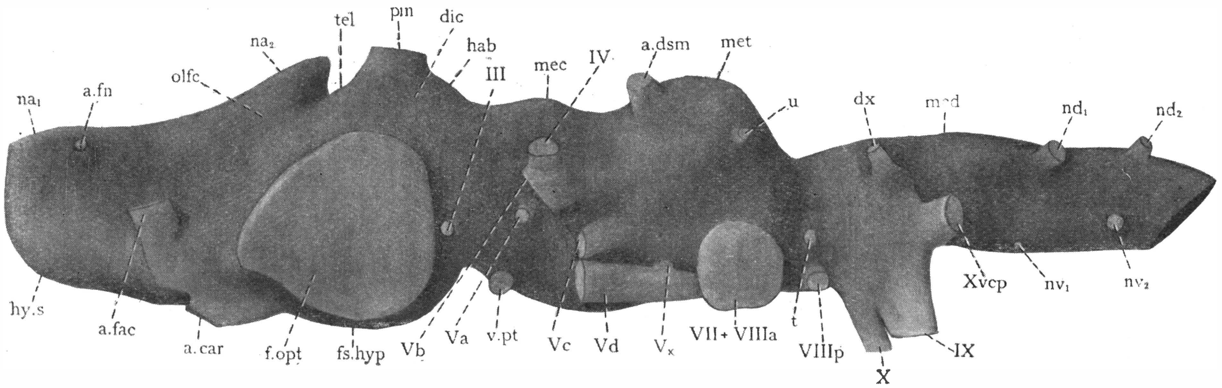
In the well preserved specimen of *Kiaeraspis* figured in pl. 52 the canal X_{br_1} just described gives off a rather strong branch lettered X_{br_1v}. This branch, which takes a postero-latero-ventral course through the ventral wall of the region, goes to the oralo-branchial chamber, opening into that chamber somewhat postero-dorso-medially to the canal X_{b_1r}. Since, as we shall see, a correspondingly situated branch issues from each one of the canals for branchial nerves in front, that is to say from each one of the canals for the n. glossopharyngeus, n. facialis etc., and since this branch evidently must have been traversed by a visceral nerve branch to the pharynx, it is very likely that the branch here under consideration in *Kiaeraspis* also had a similar function, i. e., that it gave passage to the visceral ramus from the first branchial branch of the n. vagus.

In the most postero-lateral part of the ventral wall of the region there is, in the specimen of *Cephalaspis arcticus* figured in pl. 28, an additional canal, which must be dealt with here. This canal, which is lettered *vz*, is short and rather wide and connects the canal for the first branchial branch of the n. vagus (X_{br_1}) with the canal for the a. subclavia (*a. subcl*) in the postbranchial wall. Since it is present both on the right and on the left sides, it seems to be no occasional structure. It probably transmitted an artery; but whether this artery was an efferent branchial artery or merely a nutrition artery to the posterior parts of the oralo-branchial chamber must remain undecided so far.

The dorsal wall of the region, if we next pass to that, is as a whole thicker than the ventral one. In its dorso-medial part there is always the complex system of canals, that forms the dorsal electric field (*dsf*, section series A, nos. 56—99; section series B, nos. 1—38; section series C, nos. 1—30; pls. 17, 39). It is pierced by several other canals which will more conviniently be described in anathor connection below.

Finally, each lateral wall is thick and strong as a whole, a condition which is due to the fact that it lodged the strongly developed labyrinth cavity (section series A, nos. 44—91; section series B, nos. 1—38; section series C, nos. 23—99; section series D, nos. 1—47; section series E, nos. 4—15; section series F, nos. 1—5; etc.). It gets considerably lower, however, most laterally on the lateral side of the labyrinth cavity, where it is continuous with and passes over into the visceral endoskeleton. On it we find both the anterior and posterior surfaces of the region.

From the description of the occipital region (pp. 52—56, 61) we have learned that the roots of the n. glossopharyngeus, on leaving the cavum cerebrale cranii, entered the vagus canal together with the vagus roots and the vena cerebralis posterior. And from the same description we have also seen that in certain cases they accompanied the vagus roots to the distal opening of the glossopharyngeus-vagus branch of the vagus canal, while in other cases they had their exit from the vagus canal through a branch of their own. After having thus emerged from the neurocranium posteriorly to the posterior surface of the otic region and posteriorly also to the postbranchial wall and the oralo-branchial chamber (text-figs. 13, 14), they became ganglionic; and accordingly their ganglionic complex lay posteriorly to the otic region and posteriorly to both the postbranchial wall and the oralo-branchial chamber. After its origin from the ganglionic complex the n. glossopharyngeus went first for a certain distance laterally along the posterior surface of the region, after which it turned anteriorly and penetrated into the lateral wall of the region through the canal IX*p* (text-figs. 13, 14, 18, 19, 26, 28; section series A, nos. 52—56; section series B, nos. 10—18; section series D, nos. 3—7; pl. 25), which goes forwards in an antero-lateral direction to the labyrinth cavity. And at least in certain forms, as for instance *C. hoeli*, it was situated in a distinct groove during its passage along the posterior surface of the region to the canal IX*p*. Well within the labyrinth cavity it must have traversed the postero-lateral part of that, leaving it by a canal (IX *a*) which, as we shall see, perforates the most lateral part of the lateral wall and an adjacent part of the visceral endoskeleton and goes to the oralo-branchial chamber more or less far antero-laterally to the orbital prominence.



Text-fig. 17. *Cephalaspis hoeli.* Cast of the cavum cerebrale cranii in lateral view. Model made in wax after section series A. Magnification about 17/1.

a. car, canal for the carotid artery; *a. dsm*, canal for the postorbital superficial artery; *a. fac*, canal for the arteria facialis; *a. fn*, canal for a branch from the facial artery to the external opening of the hypophyseal sac; *dic*, division of the cavum cerebrale for the diencephalon; *dx*, canal for an artery or a nerve to the posterior part of the dorsal electric field or for both an artery and a nerve; *f. opt*, optic fenestra; *fs. hyp*, hypophysial fossa, which most ventrally lodged also the posterior parts of the hypophysial sac; *hab*, bulge for the habenular ganglia; *hy. s*, division of the ethmoidal cavity for the hypophysial sac; *mec*, division of the cavum cerebrale cranii for the mesencephalon; *med*, division of the cavum cerebrale for the medulla oblongata; *met*, division of the cavum cerebrale for the cerebellum; na_1, external opening of the hypophysial sac; na_2, nasal opening proper; nd_1, canal for the myelonal vein 1 and probably also for the dorsal root of the spino-occipital nerve 1; nd_2, canal for the myelonal vein 2 and probably also for the dorsal root of spino-occipital nerve 2; nv_1, canal for the myelonal artery 1 and probably also for the ventral root of spino-occipital nerve 1; nv_2, canal for the myelonal artery 2 and probably also for the ventral root of spino-occipital nerve 2; *olf. c*, olfactory capsule; *pin*, canal for the epiphysis; *t*, *u*, canals probably for vessels; *tel*, division of the cavum cerebrale cranii for the telencephalon; *v. pt*, canal probably for the pituitary vein; III, canal for the n. occulomotorius; IV, canal for the n. trochlearis; V*a*, canal probably for the supposed viscero-motor root of the n. profundus; V*b*, canal for the general cutaneous root of the n. profundus; V*c*, canal for the general cutaneous root of the n. trigeminus proper; V*d*, canal for the viscero-motor root of the n. trigeminus proper and probably also for the n. abducens; V*x*, canal leading from the cavum cerebrale cranii to the posterior part of the canal V*d*. Probably for a nerve root; VII+VIII *a*, canal for the n. facialis, for the prootic lateralis fibres, for the electric fibres to the electric fields and for the anterior branch of the n. acusticus; VIII*p*, canal for the posterior branch of the n. acusticus; IX, branch of the vagus canal for the glossopharyngeus roots; X, branch of the vagus canal for the vagus roots; X*vcp*, branch of the vagus canal for the vena cerebralis posterior.

As is thus seen from the account given of its course, the n. glossopharyngeus traversed the labyrinth cavity, as it does in several recent fishes with a well developed labyrinth.

The most posteriorly situated canal which regularly issues from the cavum cerebrale cranii in the region is the one lettered in the figures VIII*p* (text-figs. 15—22, 24, 28; section series A, nos. 57—59; section series B, nos. 12—17, 19; section series C, nos. 50—52; section series D, nos. 4—9; pls. 25, 26, 49, 50). This canal, which is always situated close in front of the vagus canal, is short and has a rather narrow lumen. It leaves the cavum cerebrale rather close to the bottom and pierces the lateral wall of the region in a lateral and slightly posterior direction, opening into the postero-ventro-medial part of the labyrinth cavity (text-figs. 18, 19) close antero-ventrally to the bulge for the ampulla posterior (*am. post*). From its relation to the labyrinth cavity it seems highly probable that it transmitted a posterior branch of the n. acusticus to the ampulla posterior and perhaps to certain other posterior parts of the labyrinth, accordingly a branch which seems to have corresponded to the r. saccularis acustici of the recent Myxinoids. (RETZIUS 1881, pp. 10, 24; WORTHINGTON 1905, p. 172; AYERS & WORTHINGTON 1908, pp. 10—11). A posterior branch of the n. acusticus is, as is well known, found also in fishes.

In the specimen of *C. hoeli*, used for section series A, as well as in one specimen of *Kiaeraspis*, there is on both sides close above the canal for the posterior branch of the n. acusticus just described a still finer canal (*t*, text-figs. 15—17; section series A, nos. 56, 59; pl. 55) which also pierces the lateral wall and goes to the labyrinth cavity, opening into that cavity close above the former and thus not far in front of the bulge for the posterior ampulla Whether this canal too transmitted a branch from the n. acusticus or whether it was traversed by a vessel cannot be ascertained with full certainty; but since it perhaps is an occasional structure, the latter alternative seems to be the most probable one.

Rather close anteriorly to the canal for the posterior branch of the n. acusticus there follows a very wide but fairly short canal (VII+VIII*a*, text-figs. 15—17; 18 B, D, E; 19 A, B, D, E; 20—22, 24, 28; section series A, nos. 63—71; section series B, nos. 19—25; section series C, nos. 41—51; section series D, nos. 2—19; pls. 14, 18; pl. 19; fig. 1; pl. 23, fig. 3; pls. 25, 26, 45, 48, 49, 50, 55), which issues from the cavum cerebrale cranii immediately above the floor and goes straight laterally through the lateral wall of the region to the basal part of the labyrinth cavity. Whereas in *Kiaeraspis* this canal is considerably higher than it is broad, in *Cephalaspis hoeli* it is almost circular. From its course and position it is clear that it must have transmitted the anterior branch of the n. acusticus, but in addition to that, as we shall see, it certainly gave passage also to the n. facialis proper, to the prootic lateralis fibres and to the nerve fibres for the electric fields, which latter probably all pertained to the n. facialis. Accordingly the term acustico-facialis canal may be a propriate name for it.

The n. facialis, the prootic lateralis fibres and the electric nerve fibres thus all entered the labyrinth cavity. Their course through this cavity and the canals through which they left it will for practical reasons not be dealt with until later on in the descriptions of the labyrinth cavity and the visceral endoskeleton.

Rather far above the acustico-facialis canal there is in at least several specimens of *Cephalaspis hoeli* a paired, fine, short canal (*u*, text-figs. 15, 17, 18; section series A, nos. 66, 67; section series C, nos. 32—36) which goes in a lateral direction from the cavum cerebrale cranii through the lateral wall of the region to the labyrinth cavity, reaching this cavity a short distance posteriorly to the bulge for the ampulla anterior. In the specimen of *Kiaeraspis* used for section series D no correspondingly running canal could be detected. As the canal in question of *C. hoeli* issues very high up from the part of the cavum cerebrale that, as we shall see, lodged the cerebellum, it seems not very probable that it could have transmitted any nerve but that it instead gave passage to a vessel.

Slightly anteriorly to, but high above the acustico-facialis canal, a rather wide, paired canal lettered in the figures *a. dsm* (text-figs. 15—17, 20—23, 25—27; section series A, nos. 68—91; section series B, nos. 30—40; section series C, nos. 31—57; section series D, nos. 27—50; pls. 29, 30, 55) ascends in the Cephalaspids studied from the most dorso-lateral parts of the cavum cerebrale into the dorsal wall of the region and goes in an antero-latero-dorsal direction to the dorsal surface of the region as well as to a posterior part of the dorsal surface of the orbitotemporal region, branching frequently peripherically. At least in several cases it seems to break up into three main branches, which in their turn subdivide into fine rami. One of these three main branches ($a.\ dsm_3$) passes off postero-dorso-laterally to the superficial parts of the region dorsally and laterally to the anterior semicircular canal. This one will be called the posterior branch. The branch following next forwards ($a.\ dsm_2$), which is always short and often wide, takes a dorso-medial course and goes to the dorsal electric field, close to the lateral border of this. It will be referred to as the middle branch. Finally the third branch $a.\ dsm_1$ is sent out in an antero-dorsal direction to the superficial parts of the region laterally to the dorsal electric field and medially to the posterior half of the orbital opening. This branch will be termed the anterior branch. Either the middle or the anterior one of these three branches is usually in communication with the posterior part of a canal lettered $v.\ d_1$ in the figures (text-figs. 23, 25, 27; section series A, nos. 79—91; section series B. nos. 32—39; section series C, nos. 45—49;

section series D, nos. 35—45), which goes forward to the postero-dorso-lateral part of the orbit. (In the specimen of *Kiaeraspis* used for section series D, this canal of the left side does not anastomoze with any of the branches of the canal *a. dsm*). From the canal $v.d_1$ several branches issue in dorsal, lateral and medial directions.

The fact that the canal *a. dsm* issues so high up, from a part of the cavum cerebrale cranii (*met*, text-figs. 15—17; 20—23, 27) which, as we shall see, lodged the cerebellum, makes it very unlikely that it could have been traversed by any nerve. And since its mode of subdivision and termination are not in accordance with the opinion that it was a nerve-canal it must obviously have been traversed by a vessel. It seems at first not easy to conclude whether this vessel was an artery or a vein. The presence of several quite certain vein canals anteriorly, posteriorly and laterally to the branches of the canal *a. dsm*, the need of an artery to supply the medial part of the upper side of the otic region and the adjacent posterior part of the upper side of the orbitotemporal region as well as the most anterior parts of the dorsal electric field, and moreover also the fact that, except the canal *a. dsm*, there is no other canal leading to the said parts of the dorsal side of the endocranium that can be an arterial canal, all these conditions render it, however, fully evident that it was an artery. As its area of supply lay chiefly posteriorly to the orbital entrance I have named this artery the a. superficialis postorbitalis. As the a. superficialis postorbitalis, as thus defined, came from the cavum cerebrale cranii, it must certainly have arisen from the encephalic system of arteries. And as will be further pointed out below in another connection, it is highly probable that it is simply a dorsal part of one of the most anterior parietal arteries (cf. the chapter on the Petromyzontids below).

The canal $v.\ d_1$ must, according to its origin and course, have transmitted a vein which drained certain anterior and middle parts of the dorsal electric field and certain adjacent parts of the cranial roof. As we shall see from the account given below, this vein emptied into the vena capitis lateralis just before this vein left the orbit (cf. the description of the orbitotemporal region and the chapter on the vascular system).

In all Cephalaspids investigated by me the lateral wall of the region is pierced at least by certain of the canals (V, V*c*, V*d*, text-figs. 16, 17, 21, 22, 24, 28; section series A, nos. 70—99; section series B, nos. 19—38; section series C, nos. 1—9, 24—48; section series D, nos. 4—14; pls. 14, 18; pl. 19, fig. 1; pls. 26, 45, 49, 55) for the trigeminus roots. For practical reasons, however, I shall not deal with these canals here but postpone their treatment to the description of the orbitotemporal region. Also a second canal, the one lettered *v. pt* in the figures, despite the fact that it is given off from the bottom of the cavum cerebrale cranii above the posterior parts of the dorsum sellae and passes laterally through the lateral wall, will for practical reasons not be described until later on in connection with the orbitotemporal region.

The dorso-lateral part of the region is, close dorso-laterally to the labyrinth cavity of each side, perforated in a longitudinal direction by a wide canal, *v. cl* (text-figs. 23—28; section series A, nos. 39—84; section series B, nos. 1—38; section series C, nos. 65—81; section series D, nos. 1—33; section series E, nos. 1—14; pls. 18, 21, 23—27, 29, 44, 45, 47, 49, 50, 53, 54, 55), which goes from the postero-lateral part of the orbit to the posterior surface of the region, opening there rather close dorso-laterally to the posterior opening of the canal IX*p*, through which the n. glossopharyngeus reached the labyrinth cavity (text-figs. 13, 14). This canal *v. cl*, which throughout almost its entire length lies on or very close to the dorsal side of the vestibular division of the labyrinth cavity, laterally to the other divisions of that cavity (the anterior and posterior semicircular divisions and the commissural divisions), is bent more or less in accordance with the arching of the vestibular division and in addition so that its middle parts lie nearer to the median line than the anterior and posterior ones. Into it open several canals, which as is obvious from their distal branching (pls. 25, 29), must have transmitted vessels. From this fact and from its position and course it is not difficult to conclude that it must have been traversed by a vein corresponding to the vena capitis lateralis of *Petromyzon* and young larval stages of fishes (cf. CORI 1906, pp. 48—52; HATTA 1922, pp. 180—182; DE BEER 1924; 1926). And we are thus able to establish that the v. capitis lateralis persisted and played a very important part in the adult Cephalaspids.

After having now described the canal for the v. capitis lateralis, we shall next pass to the canals which joined that canal and which accordingly gave passage to tributaries to the v. capitis lateralis.

The most posterior one of the canals which joined the canal for the v. capitis lateralis is the occipital vein sinus. As has been pointed out already above in the description of the occipital region, this sinus (*vs. oc*, text-figs. 23—28; section series A, nos. 25—46; section series B, nos. 1—15; section series C, nos. 48—73; section series D, nos. 1—42; pl. 23, fig. 1; pls. 25, 26, 29, 49; pl. 54, fig. 1; pl. 55) is situated in the lateral wall of the endocranium at the transition between the occipital and otic regions. The communication between it and the canal for the v. capitis lateralis always takes place on the medial or dorso-medial side of the last mentioned canal, at or close in front of the posterior end of this.

Into the occipital vein sinus opens on the anterior side the wide canal *v. dsv* (text-figs. 23, 26, 27; section series A, nos. 47—49; section series B, nos. 7—18; section series C, nos. 31—51; section series D, nos. 24—38; pl. 13, fig. 3) which, as we have seen, comes from the labyrinth cavity and a canal issuing in a dorsal direction from that cavity and which goes in a postero-lateral direction through the lateral wall of the region. As for the understanding of the function of this canal it is necessary to enter upon certain details of the labyrinth cavity a detailed description of it can only be given in connection with the account of that cavity.

The dorsal (external) surface of the parts of the visceral endoskeleton situated laterally to the otic and orbitotemporal regions is, as we shall see further from the account below, drained by four segmentally disposed veins, termed the dorso-lateral superficial veins 3—6, which all went dorso-medially and emptied their blood into the v. capitis lateralis. In the simplest cases these veins were certainly independent of each other throughout their extent and accordingly they also emptied into the v. capitis lateralis independently of each other. In the forms known in detail, however, we do not find so simple conditions any more, but certain of the four veins in question had most dorso-medially in the vicinnity of the v. capitis lateralis joined each other.

After these general remarks we can now turn to a more detailed account of the canals for the four dorso-lateral superficial veins in question. These canals, which according to their position from in front backwards are lettered in the figures $v.\ ls_3$, $v.\ ls_4$, $v.\ ls_5$, and $v.\ ls_6$ respectively, are often distinctly preserved (text-figs, 46—51; pls. 17, 18, 20, 24—30, 39, 45, 47, 49, 50, 54, 55, 57). The most posterior one of them ($v.\ ls_6$) always joins the canal for the v. capitis lateralis somewhat in front of the occipital vein sinus above the posterior part of the labyrinth cavity. On the other hand, the most anterior one ($v.\ ls_3$) goes, in certain forms such as *Kiaeraspis* and *Hoelaspis*, also to the canal for the v. capitis lateralis, opening into that canal close behind the orbit, while in other forms, such as the *Cephalaspis* species, it always passes to the most postero-ventro-lateral corner of the orbit. As it is clear, however, that in the latter case the vein which traversed the canal $v.\ ls_3$ must have emptied into the v. capitis lateralis in the very posterior part of the orbit, it is obvious that the conditions in this respect in the *Cephalaspis*-species were not essentially different from those in *Kiaeraspis* and *Hoelaspis.* And we are thus able to establish that both the dorso-lateral-superficial vein transmitted by the canal $v.\ ls_6$ and that which had its passage through the canal $v.\ ls_3$ always emptied directly into the v. capitis lateralis. In *Hoelaspis* (pl. 45) the canal $v.\ ls_4$ also reaches as far dorsally as to unite direct with the canal for the v. capitis lateralis, while in all other forms the two canals $v.\ ls_4$ and $v.\ ls_5$ never open directly into the last-mentioned canal but unite in various ways with $v.\ ls_3$ and $v.\ ls_4$ or with one or another of these. Thus in *Cephalaspis heintzi* (text-fig. 46, pls. 29, 30), $v.\ ls_4$ and $v.\ ls_5$ join $v.\ ls_3$, while in *C. vogti* (text-figs. 47, 48; pls. 25, 27), on the contrary, they join instead $v.\ ls_6$. In other forms, as *Kiaeraspis* (text-fig. 28; pl. 55) and *C. spitsbergensis* (text-fig. 49; pl. 39), the canal $v.\ ls_4$

unites with *v.* ls_3 and *v.* ls_5 with *v.* ls_6. In *C. hoeli* the conditions with regard to the canals *v.* ls_4 and *v.* ls_5 are in certain specimens as in *C. vogti* (pl. 24, fig. 1), in other specimens, on the contrary, as in *Kiaeraspis* and *C. spitsbergensis.* Finally in *Hoelaspis* the canal *v.* ls_5 unites with *v.* ls_6, while, as already pointed out, *v.* ls_4 goes independently to the canal for the v. capitis lateralis.

In those cases where the canal *v.* ls_4 alone or both *v.* ls_4 and *v.* ls_5 join the canal *v.* ls_3 the proximal part of the latter is in the text-figures and plates mostly denoted by the letters *v. la.* On the other hand in those cases where the canal *v.* ls_5 alone or both *v.* ls_5 and *v.* ls_4 join the canal *v.* ls_6, the proximal part of the latter is in the text-figures and plates lettered *v. lp* (cf. text-figs. 23—28; 46—51).

Besides the tributaries already dealt with, the vena capitis lateralis received during its passage through the canal *v. cl* also certain others from the superficial parts of the region above and between the anterior and posterior semicircular canals and from the underlying vestibular division of the labyrinth cavity.

The former of these tributaries, which traversed the canals *v. ds*, *v.* ds_1 and *v.* ds_2 (text-figs. 23, 25, 26, 27; section series A. nos. 56, 59, 67, 70; section series B, nos. 21; section series D, nos. 34—47; section series E, no. 10; pls. 29, 30), obviously collected the blood which was distributed by the most peripheral ramuli of the posterior branch of the arteria superficialis postorbitalis, that is to say the artery issuing from the cavum cerebrale through the canal *a. dsm.* These tributaries opened into the vena capitis lateralis on the dorso-medial or dorsal side and were as a rule only two in number. The tributaries from the vestibular division of the labyrinth cavity which had their passage through a number of fine canals lettered *v. lab*, or *v.* lab_1, *v.* lab_2, etc. (text-figs. 18, 19; section series A, nos. 57—67; section series B, nos. 18, 24, 25, 27—29; section series C, nos. 65—70; section series D, nos. 12—14; 19, 20, 26; section series E, no. 7; pl. 26), were mostly very fine. Their number varied from 2 to 4 or 5 and they always reached the vena capitis lateralis on the ventral or ventro-medial side. In this connection it ought to be specially emphasized that in one specimen of *Cephalaspis hoeli* the canal for the v. capites lateralis (*v. cl*) for a certain stretch was in open communication with the underlying vestibular division of the labyrinth cavity (text-fig. 18 D; section series A, nos. 58—67). Concerning the canals *v. lab, v.* lab_1, *v.* lab_2, etc. it is to be added here that, in addition to small veins, they may also perhaps have been traversed by fine nerve branches from the n. glossopharyngeus and the n. facialis and the lateralis fibres accompanying these nerve, fine nerve branches which may have supplied the upper surface of the region and certain parts of the lateral sensory canals situated on the exoskeleton that covers the region.

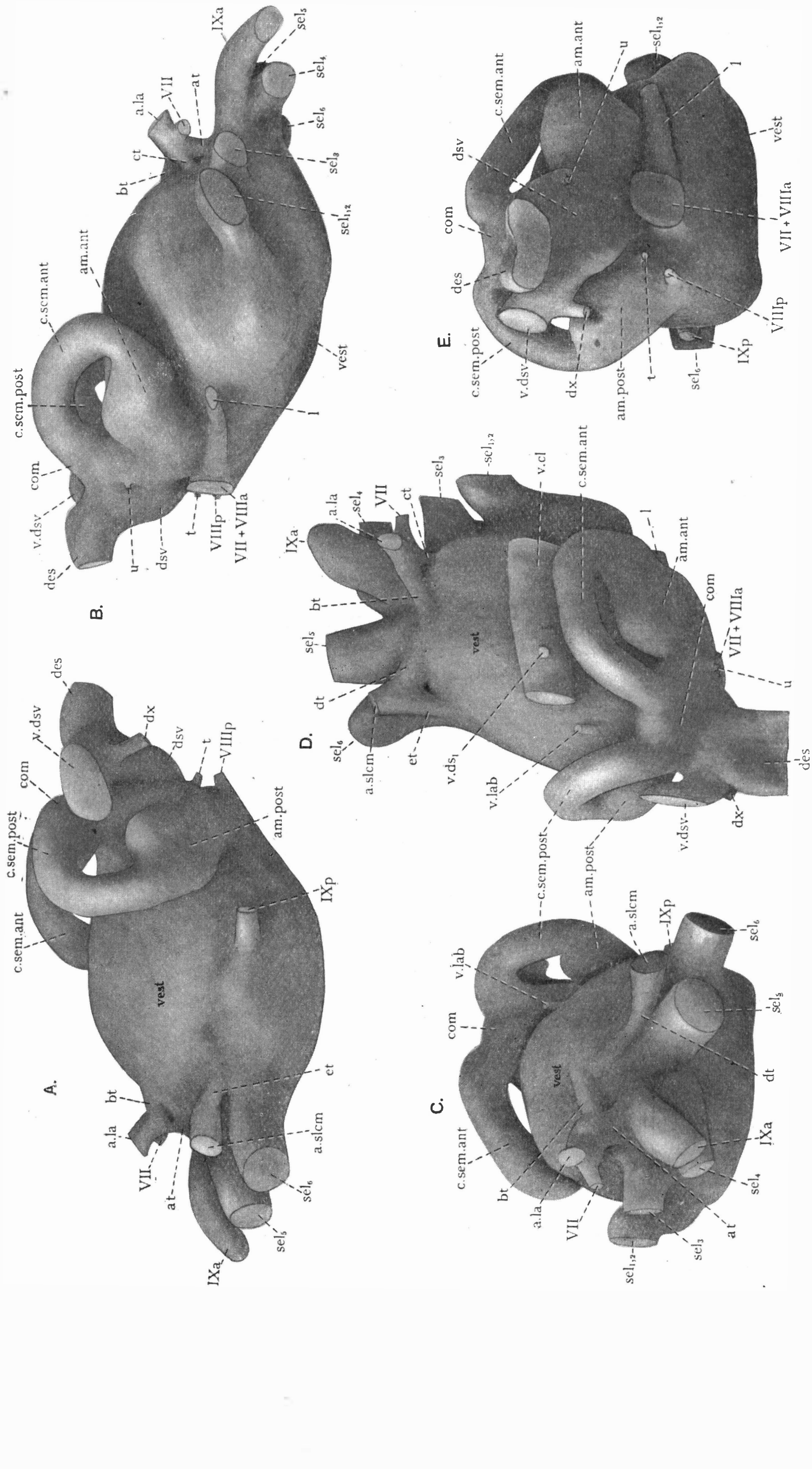
In the most anterior and lateral parts of the region anteriorly and laterally to the labyrinth cavity there are, besides the venous canals described, several other canals for arteries and nerves. Since these canals all issue from the labyrinth cavity they must be described in detail in the account given below of the cavity.

Labyrinth cavity. — As is shown by text-figs. 18, 19, 23—28 and several of the plates (pl. 18; pl. 19, fig. 1; pls. 21, 25, 26, 28, 44, 49, 50, 55) the labyrinth cavity is of a considerable size. It is well separated from the cavum cerebrale cranii, being in communication with this only by the canals for nerves and vessels leading to it. As has already been pointed out above (p. 30), it is lined by a perichondral bone-layer of its own, the labyrinth bone-layer, which by means of canal layers is continuous with the internal perichondral bone-layer, with the external perichondral bone-layer and with the basal layer of the exoskeleton. Its position within the lateral wall of the otic region is well displayed by the section series, especially by the series A, B, C and D.

The labyrinth cavity consist of four distinct divisions: the vestibular division, the commissural division, the anterior semicircular division and the posterior semicircular division.

The vestibular division (*vest*, text-figs. 18, 19, 23—28; section series A, nos. 54—91; section series B, nos. 1—37; section series C, nos. 41—97; section series D, nos. 1—27; pl. 13, figs. 2, 3; pls. 14, 18; pl. 19, fig. 1; pl. 21; pl. 23, fig. 3; pls. 24, 25, 26, 28, 44, 45; pl. 46, fig. 1; pl. 47, fig. 1; pls. 49, 50, 52, 55), if we first turn to that, forms the basal and lateral part of the labyrinth cavity. It is always big, sometimes even so big that it may considerably exceed in volume the other three divisions together. In *Boreaspis rostrata* (pl. 13, figs. 2, 3; pl. 14) it seems to have been almost circular in outline, when seen from above or below. In the majority of forms in which it is known so far, as, for instance, the *Cephalaspis*-species, *Hoelaspis* and *Kiaeraspis*, on the contrary, it is always more extended in the transversal than in the rostro-caudal direction, i. e. it is in these forms broader than it is long. Its maximum height, which was approximately equal to the maximum length (measured in rostro-caudal direction), was, at least in *Kiaeraspis* and *Cephalaspis hoeli*, situated somewhat laterally to the middle.

The commissural division (*com*, text-figs. 18, 19, 23, 25—27; section series A, nos. 52—66; section series B, nos. 16—29; section series C, nos. 41—59; section series D, nos. 15—45; pl. 13, fig. 3; pls. 17, 29, 39), which is known in detail only in *Kiaeraspis* and in *Cephalaspis hoeli*, issues from the middle and dorsal parts of the medial side of the vestibular division in a dorsal or somewhat latero-dorsal direction. As is well shown by text-figs. 18 and 19, it is relatively higher and narrower in *Kiaeraspis* than in *Cephalaspis hoeli*, but in both these



Text-fig. 18. *Cephalaspis hoeli.*

Text-fig. 18. *Cephalaspis hoeli.* Cast of the labyrinth cavity. Wax model made after section series A $^{15}/_{1}$. *A* in posterior, *B* in anterior, *C* in lateral, *D* in dorsal and *E* in medial views. $^{15}/_{1}$.

a. la, common canal for the two anterior dorso-lateral superficial arteries; *a. slcm*, canal for the two posterior dorso-lateral superficial arteries; *am. ant*, swelling for the ampulla anterior; *am. post*, swelling for the ampulla posterior; *at*, *bt*, canals for the n. facialis and for the two anterior dorso-lateral superficial arteries; *c. sem. ant*, division of the labyrinth cavity for the canalis semicircularis anterior; *c. sem. post*, division of the labyrinth cavity for the canalis semicircularis posterior; *com*, commissural division of the labyrinth cavity; *ct*, canal for a branch from the n. facialis or for a branch from one of the anterior dorso-lateral superficial arteries; *des*, canal for the electric nerves to the dorsal electric field and in addition at least for a vein from that field; *dsv*, groove for the electric nerve to the dorsal electric field; *dt*, *et*, canals for the posterior dorso-laterial superficial arteries; *dx*, canal for an artery, or for a nerve from the glossopharyngeus-vagus complex to the dorsal electric field or for both these structures; *l*, canal for the passage of certain of the prootic lateralis fibres to the orbit; $sel_{1,2}$, common canal for the two most anterior nerves to the lateral electric field; sel_3—sel_6, canal for the third, fourth, fifth and sixth nerves to the lateral electric field; *t*, *u*, canals probably for vessels; *v. cl*, canal for the vena capitis lateralis (a middle part only shown); *v. dsv*, canal for the otical vein. This canal probably lodged also the ductus endolymphaticus; *vest*, vestibular division of the labyrinth cavity; *v ds*, canal for a dorsal tributary to the v. capitis lateralis; *v. lab*, canal for a venous branch from the vestibular division of the labyrinth cavity to the vena capitis lateralis and in addition perhaps for nerve branches to the dorsal side of the otic region; VII, canal through which the n. facialis left the vestibular division of the labyrint cavity; VII+VIII *a*, canal for the n. facialis, the electric nerve fibres, the prootic lateralis fibres and in addition at least for the anterior branch of the n. accusticus (the r. saccularis accusticus or a part of that); VIII *p*, canal for the posterior branch of the n. accusticus; IX *a*, canal through which the n. glossopharyngeus lefth the labyrinth cavity; IX *p*, canal through which the n. glossopharyngeus entered the labyrinth cavity.

forms the height is, however, always its greatest dimension. Its breadth (diameter in transverse direction) is most dorsally rather small but gets somewhat larger downwards. Its extension in a rostro-caudal direction is, in *Cephalaspis hoeli*, also somewhat larger ventrally than dorsally, while in *Kiaeraspis* it remains approximately the same throughout the height.

Finally the anterior and posterior semicircular divisions (*c. sem. ant*, and *c. sem. post*, text-figs. 18, 19, 23—28; section series A, nos. 44—54, 66—87; section series B, nos. 1—18, 21—38; section series C, nos. 52—69; section series D, nos. 2—47; pls. 13, 17—19, 24, 29, 39, 44, 45, 47, 49), though displayed in many specimens, could, however, be studied in detail only in the specimens of *Kiaeraspis* and *Cephalaspis hoeli* used for serial sections. They are both very distinct and well bounded and both issue from the medial end of the vestibular division, the anterior one (*c. sem. ant*) just anteroventrally, and the posterior one (*c. sem. post*) just postero-ventrally to the commissural division. At their origin, however, both are in communication also with the commissural division. Just after their origin from the vestibular division each of them has al arge swelling (*am. ant*, and *am. post*) evidently for its ampulla. With their upper end they join the dorsal end of the commissural division. Concerning their position it is noteworthy that they stand so that they form with each other an angle which is somewhat less than a right angle. The anterior one is otherwise inclined somewhat postero-latarally, the posterior one, on the contrary, somewhat antero-laterally and both therefore occupy a position as if they have been somewhat pressed downwards towards each other and towards the vestibular division. Especially in *Cephalaspis hoeli* this condition is well seen. But both in that species and in *Kiaeraspis* the two semicircular divisions are, however, very independent in relation to the vestibular division.

The dorsal end of the commissural division and the dorsal parts of the semicircular divisions are situated very close beneath the exoskeleton and in places they may even be in contact with that. At these places their lining perichondral bone-layer seems to be fused with the basal laminated layer of the exoskeleton.

There is no division of the labyrinth cavity that could have lodged any canalis semicircularis externus.

From the shape and mutual relations of the different divisions of the labyrinth cavity now described it is not difficult to see that the membranous labyrinth cannot have been like that in fishes or Tetrapods but that it must have been of a type very similar to that found in the recent Petromyzontids (RETZIUS 1881, pp. 13—27; KRAUSE 1923, pp. 775—784; etc.). The vestibular division must obviously have lodged a structure closely corresponding to the vestibulum of the Petromyzontids; but whether this structure was subdivided like the vestibulum of the Petromyzontids and like that had a ventral sac-like appendage must be left undecided. Of the other division the commisural one was certainly occupied by the homologue of the commisure in Petromyzontids and the sinus utriculi superior of fishes, and the two semicircular ones by the anterior and posterior semicircular canals. The external semicircular canal was entirely absent. The anterior and posterior semicircular canals had their origin from the vestibulum quite as the corresponding canals in Petromyzontids; and, like these, were provided with ampullae, though much larger than in these. If only the two semicircular canals of the Cephalaspids had been pressed downwards and outwards until they had become situated tight to the dorsal side of the vestibulum, the conditions with regard to the membranous labyrinth as a whole would in fact have been very much the same as in the Petromyzontids. The fact, however, that the semcircular canals had a much more erect position and on account of that were more independent in relation to the vestibulum than they are in the recent Petromyzontids cannot, be considered as a feature of any great importance. And thus we may be fully justified in concluding that the membranous labyrinth of the Cephalaspids was of the Petromyzontid type.

After having now treated the different divisions of the labyrinth cavity and their functions, we turn next to the canals for nerves and vessels leading to the labyrinth cavity.

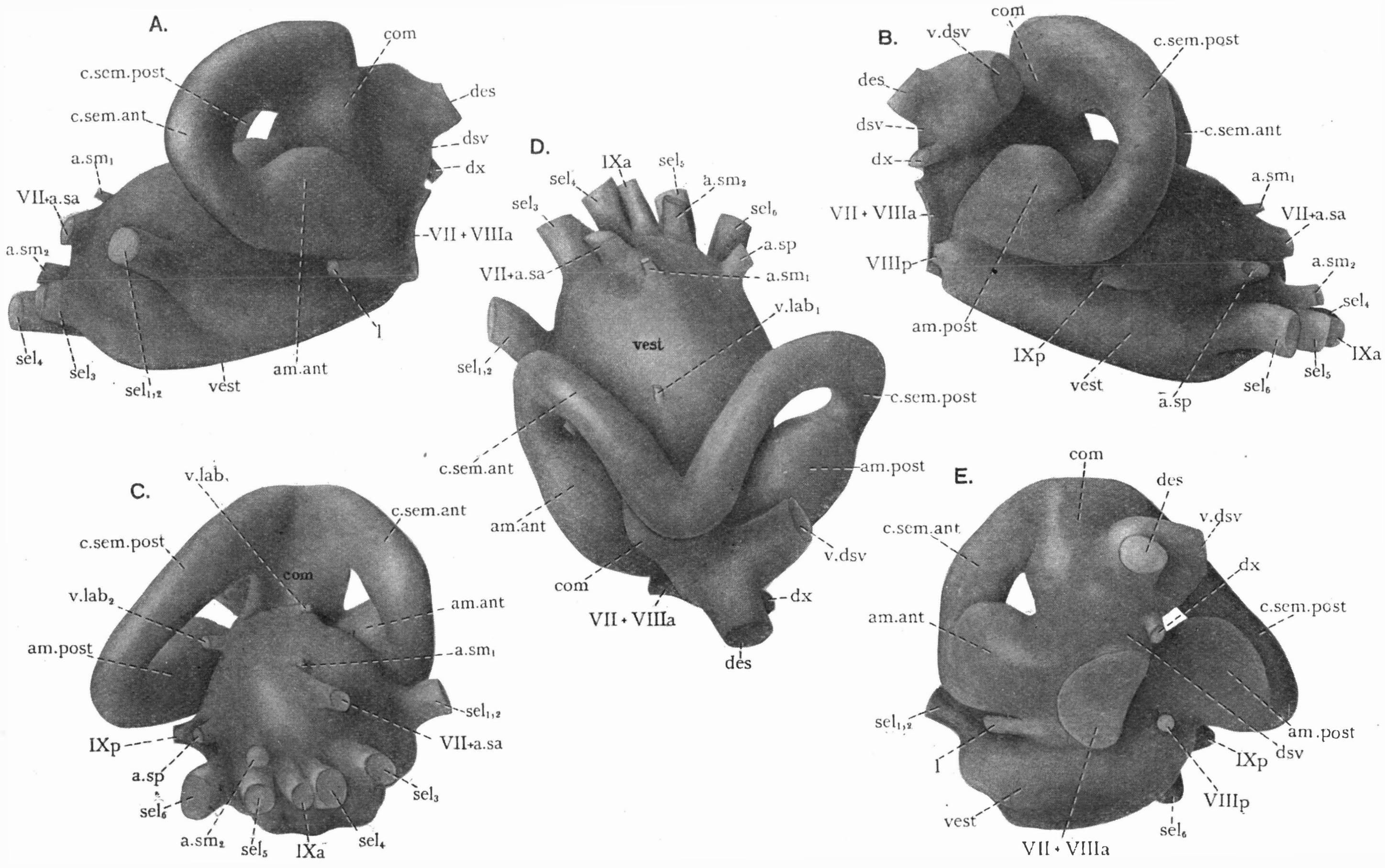
As already described above (p. 69), the n. glossopharyngeus entered the labyrinth cavity through an antero-laterally running canal (IX *p* text-figs. 13, 14, 18, 19, 24, 26, 28; section series A, nos. 52—55; section series B, nos. 17, 18; section series D, nos. 3—7; pl. 25), which opens on the posterior side of the vestibular division somewhat laterally to (*Cephalaspis hoeli*) or just beneath (*Kiaeraspis*) the most lateral parts of the posterior semicircular division. It thus had its normal relations to the canalis semicircularis posterior. From the course of its canal (IX *p*) it is seen that it can only have traversed a posterio-lateral part of the vestibular division. How it left that division will be discussed below.

The most posterior canal which goes directly from the cavum cerebrale to the labyrinth cavity is the one lettered *dx* in the figures (text-figs. 15—23, 26), already treated in the description of the occipital region (p. 57). We shall have the opportunity of returning to that canal below in this connection.

The canal which leaves the cavum cerebrale next in front of *dx* and, like that, goes to the labyrinth cavity is the canal interpreted above (p. 71) as the canal for the posterior branch of the n. acusticus (VIII *p*, text-figs. 15—22, 24, 28; section series A, nos. 57—59; section series B, nos. 12—17, 18, 19; section series C, nos. 50—52; section series D nos. 4—9; pls. 25, 26, 49, 50). This canal opens into the vestibular division low down close antero-ventrally to the origin of the posterior semicircular division or, more exactly, close antero-ventrally to the ampullary swelling of that division, a fact, which as already pointed, out makes it very probable that it gave passage to a posterior branch of the acustic nerve, supplying the posterior ampulla and perhaps the sac-like appendage of the vestibulum too, if that appendage was present.

The fine canal *t* (text-figs. 15—17, 18; section series A nos. 56, 59; which is, found with certainty only in *Cephalaspis hoeli*, and which goes from the cavum cerebrale to the labyrinth cavity slightly above the canal for the ramus saccularis acustici, seems most likely to have transmitted a vessel (cf. p. 71 above).

The most important canal which connects the cavum cerebrale cranii with the labyrinth cavity is, as we have already seen (p. 71, 72, above), the wide acustico-facialis canal (VII + VIII *a*). This canal, as is well shown by text-figs. 18 and 19 goes to the medial end of the vestibular division, opening there close above the bottom rather straight ventrally to the commissural division. Since it transmitted several important nerve-roots it is very wide and in *Kiaeraspis* also high.



Text-fig. 19. *Kiaeraspis auchenaspidoides.*

Text-fig. 19. *Kiaeraspis auchenaspidoides.* Cast of the labyrinth cavity. Photograph of a model in wax made chiefly after sections series D.

A in anterior, *B* in posterior, *C* in lateral, *D* in dorsal, and *E* in medial views. 20/1.

a. sm$_1$, and *a. sm*$_2$, canals for the dorso-lateral superficial arteries 2 and 3; *a. sp*, canal for the dorso-lateral superficial artery 4; *am. ant*, swelling for the ampulla anterior; *am. post*, swelling for the ampulla posterior; *c. sem. ant*, division of the labyrinth cavity for the canalis semicircularis anterior; *c. sem. post*, division of the labyrinth cavity for the canalis semicircularis posterior; *com*, commissural division of the labyrinth cavity; *des*, canal for the nerve to the dorsal electric field and in addition at least for a vein from that field; *dsv*, groove for the electric nerve to the dorsal electric field; *dx*, canal for an artery or for a nerve from the glossopharyngeus-vagus complex to the dorsal electric field or for both these structures; *l*, canal for the passage of certain of the prootic lateralis fibres to the orbit; *sel*$_{1,2}$, common canal for the two most anterior electric nerves to the lateral electric field; *sel*$_3$—*sel*$_6$, canals for the third, fourth, fifth, and sixth electric nerves to the lateral electric field; *v. dsv*, canal for the otical vein. This canal probably lodged also the ductus endolymphaticus; *v. lab*$_1$, *v. lab*$_2$, canals for venous branches from the vestibular division of the labyrinth cavity to the vena capitis lateralis and in addition probably also for nerve branches to the dorsal side of the otic region; *vest*, vestibular division of the labyrinth cavity; *VII+a. sa*, the canal through which the n. facialis and the dorso-lateral superficial artery 1 left the vestibular division of the labyrinth cavity; VII + VIII *a*, canal for the n. facialis (+the electric fibres), the prootic lateralis fibres and in addition at least for the anterior branch of the n. accusticus; VIII *p*, canal for the posterior branch of the n. acusticus; IX *a*, canal through which the n. glossopharyngeus left the labyrinth cavity; IX *p*, canal through which the n. glossopharyngeus entered the labyrinth cavity.

Finally, the canal *u*, which has been found only in *Cephalaspis hoeli*, goes from the cavum cerebrale cranii to the antero-ventral part of the commissural division (text-figs. 15, 17, 18 B, D, E; section series A nos. 66, 67; section series C nos. 31—36) rather close posteriorly to the ampullary swelling *(am. ant)* of the anterior semicircular division. Since, as has been emphasized above (p. 72), it leaves the cavum cerebrale strikingly high up on the side of the part of this that lodged the cerebellum, it seems very improbable that it was traversed by a nerve. As far as can be judged, we would thus here be concerned with a canal for a vessel.

The canals which lead out from the labyrinth cavity are more numerous than those leading to it. And as can easily be understood from their course and branching, certain of them were nerve-canals, while others transmitted vessels.

From the lateral and antero-lateral parts of the vestibular division of the labyrinth cavity there issue regularly five wide canals *sel*$_{1,2}$, *sel*$_3$, *sel*$_4$, *sel*$_5$, and *sel*$_6$, (text-figs. 18, 19, 23—28; section series A nos. 56—92; section series B, nos. 2—38; section series C, nos. 68—105; section series D, nos. 1—3; pls. 14, 21, 28, 44, 45, 49, 50, 52), which commence as distinct grooves (appearing as rounded ridges in the casts) on the floor of the vestibular division. As these canals all go to the lateral electric field and break up there into a great number of fine branches in the way shown in pls. 29 and 30, it is quite obvious that they lodged the nerves to the lateral electric field.

The most anterior, $sel_{1,2}$, (text-figs. 18, 19, 23—25, 27, 28; pls. 14, 18, 21, 28, 45, 49, 50) of these nerve canals leaves the vestibular division on the anterior side rather high up and is, in *Kiaeraspis*, situated rather far in front of the other four. The groove on the floor of the vestibular division that leads to this canal is always more pronounced than those leading to other canals of the same kind. And as the canal in question is sent out from the vestibular division more proximally than those canals, the groove leading to it also begins more proximally than the grooves leading to the other ones. The canal which after its origin first goes anteriorly to the part of the orbitotemporal region situated immediately laterally to the orbit will be further treated in the descriptions given below of that region and of the visceral endoskeleton. Here it should only be added that whereas the canals sel_3 and the other ones following behind it were all traversed only by one nerve, the canal $sel_{1,2}$ transmitted instead two nerves which separated from each other more or less far before their entrance into the lateral electric field. As a consequence of this, the canal $sel_{1,2}$ bifurcates more or less soon anteriorly or antero-laterally to the orbit during its passage through the visceral endoskeleton. In the different forms the conditions regarding this bifurcation are as follows: in the *Cephalaspis*-species it takes place close antero-ventro-laterally to the orbit (sel_1 and sel_2, text-figs. 23—25, 46; pls. 17, 18, 20, 21, 27, 28, 29), in *Benneviaspis* (pl. 42, fig. 2) approximately midway between the orbit and the lateral electric field; in *Boreaspis rostrata* and *Hoelaspis* rather far antero-ventro-laterally to the orbit (sel_1 and sel_2, pls. 14, 45) and thus rather near to the lateral electric field; and finally in *Kiaeraspis* (text-fig. 28, sel_1, and sel_2, pls. 49, 50) first close laterally to or perhaps even within the lateral electric field. Of the other four nerve canals leading to the lateral electric field the three anterior ones, soon after leaving the vestibular division of the labyrinth cavity, enter the visceral endoskeleton (text-figs. 28, 46, 47; pls. 14, 21, 27, 28, 29, 44, 45, 49, 50). The most anterior one (sel_3) of them goes antero-laterally, the next one (sel_4) still more laterally or almost straight laterally, the third one from in front (sel_5) straight laterally or slightly posteriorly. Finally, the most posterior one (sel_6) takes a postero-lateral course through the most antero-lateral parts of the occipital region (text-fig. 13) and from that through the dorsal part of the endoskeletal shoulder-girdle (text-fig. 13) to the hindmost part of the lateral electric field.

Immediately dorsally to the opening of the acustico-facialis canal into the labyrinth cavity there begins on the medial side of the vestibular division a very distinct, broad and strong groove (*dsv*, text-figs. 18,

19. Since these figures are casts of the labyrinth cavity, however, the groove in question appears in them as a ridge; section series A, nos. 53—63; B, nos. 19—23; D, nos. 17—29 pl. 18; pl. 19, fig. 1). This groove continues upwards on the medial side of the commissural division, gradually increasing in depth upwards and finally at about the middle of the height of the commissural division suddenly separating from that as a wide canal, which, immediately divides into two the canals, a dorso-medial one, *des*, and a posterior one, *v. dsv*.

The dorso-medial one, *des*, (text-figs. 18, 19, 23, 26, 27; section series A, nos. 50—60; section series B, nos. 17—23; section series C, nos. 1, 23—40; section series D, nos. 30—35; pl. 29) of these two canals, which is always wide, goes in a medial and somewhat dorsal direction to the deepest part of the dorsal electric field, in which it meets and joins its fellow of the opposite side. From the common trunk thus formed by the union of the right and left canals *des* in question thick branches issue both anteriorly and posteriorly on the bottom of the dorsal electric field; and these thick branches in their turn ramify frequently in the way shown in pls. 17 and 39 and the section series B. Accordingly the canal *des* has similar relations to the dorsal electric field as the nerve-canals to the lateral electric field and as in addition there is no other canal through which nerves could have reached the dorsal electric field, we may conclude with full certainty that the canal *des* transmitted the nerve to that electric field. In addition it may have been traversed also by an artery to and a vein from that electric field.

The posterior canal, *v. dsv*, (text-figs. 18, 19, 23, 26, 27; section series A, nos. 47—49; section series B, nos. 7—18; section series C, nos. 31—52; section series D, nos. 24—40; pl. 13, fig. 3), arising from the groove *dsv*, always takes a postero-lateral course and goes to the antero-dorso-medial part of the occipital vein sinus, a state of things which shows that it must have lodged a vein. As is seen from text-fig. 23 and text-fig. 27, the canal has such relations to the nerve canal *des* for the dorsal electric field that the vein it transmitted — which, as has already been pointed out above, will be called the otical vein — may very well by thought to have drained a considerable middle part of the dorsal electric field. In addition, as is seen from text-figs. 18 E and 19 E, the canal quite clearly continues downwards into the groove *dsv*, so that the vein lodged by it must perhaps have received a tributary also from the labyrinth. The venous blood from a middle part of the dorsal electric field and certain medial parts of the labyrinth thus seems to have emptied into the occipital vein sinus from which, as we have seen, it was brought into the vena capitis lateralis.

In this connection attention must also from another point of view be called to the fact that the canal *v. dsv* here in question is distinctly continuous downwards with the groove *dsv*. Above (p. 62), when dealing with the posteriorly produced corner of the occipital vein sinus and the canal d_1 leading from this, it was pointed out that the latter canal, owing to its mode of opening on the dorsal side of the exoskeleton of the cephalic shield in certain forms, such as *Thyestes verrucosus*, can hardly have been simply a vein-canal, but that there was reason to assume that the ductus endolymphaticus reached up to the dorsal surface of the head through it. It is highly interesting to find that the canal d_1 by means of the occipital vein sinus and the canal for the otical vein (*v. dsv*) at least in the fossil in fact therefore is in open communication with the dorso-medial parts of the labyrinth cavity. We may therefore probably consider it as fairly certain that the ductus endolymphaticus persisted as an important organ, which conceivably opened outwards on the dorsal side of the head and that its most dorsal part was situated in the canal d_1.

The canal *dx* already referred to above (pp. 57, 81) opens in *Kiaeraspis* (text-fig. 19 B, E) in the groove *dsv* close below the canal *v. dsv*, in *Cephalaspis hoeli* (text-fig. 18 A, E), on the contrary, just at the beginning of the canal *v. dsv*. As already described it issues from the dorsal side of the cavum cerebrale cranii opposite the canal for the occipital artery (*c. post*, text-figs. 14—17, 20—22, 24, 28) and close medially to the internal opening of the vagus canal, and, as far can be judged from its course and position, it may thus have given passage either to a dorsal artery for the dorsal electric field — a branch from the occipital encephalic artery — or to a nerve branch consisting of general cutaneous fibres and perhaps also of lateralis fibres all of which went to the dorsal side of the head. It is of course not excluded that it transmitted both an artery and a nerve branch.

From the opening of the acustico-facialis canal into the labyrinth cavity a rather narrow but nevertheless very distinct groove leads forward on the medial surface of the vestibular division (text-figs. 18 B, E; 19 A, E; section series A, nos. 71—76; section series B, nos. 22, 23, 29; section series C, nos. 49—55; section series D, nos. 8, 9). This groove, which is situated close below the swelling for the ampulla anterior, leads into an antero-laterally running canal (*l*, text-figs. 18 B, E; 19 A, E: 24; section series A, nos. 77—93; section series B, nos. 24—28, 30, 31; section series C, nos. 56—66; section series D, nos. 2—4, 10; pl. 14; pl. 19, fig. 1; pl. 23, fig. 3; pls. 25, 26, 49, 50, 55), which goes to the postero-ventro-medial part of the orbit. This canal and the groove leading to it obviously gave passage to a structure which entered the vestibular division of the labyrinth cavity through the acustico-facialis canal and then immediately turned forwards and went to the orbit. From its course and relations it seems highly probable that the canal and the groove were traversed by a nerve which corresponded to the one which in *Petromyzon* (text-fig. 38; cf. AHLBORN 1884, p. 300: pl. 18, fig. 5; HATSCHEK 1892, fig. 11; JOHNSTON 1905, pp. 157—163, pl. 5: 1908; etc.) passes from the otic capsule to the orbit and which consists of the lateralis fibres which accompany the trigeminus branches. And we thus find that, as far as can be judged, the lateralis fibres both for the n. trigeminus and for the n. facialis accompanied the latter nerve from the cavum cerebrale and that together with that they entered the vestibular division of the labyrinth cavity.

Between the nerve canals sel_4 and sel_5 for the lateral electric field and in several cases slightly dorsally to these canals a wide canal, IX *a*, (text-figs. 18; 19; 23—25, 27, 28; section series A, nos. 65—92; section series B, nos. 18—25; section series C, nos. 96—109; pl. 20; pl. 24, fig. 2; pls. 28, 29, 30, 44, 49, 50, 51, pl. 54, fig. 1, pl. 57; pl. 62, fig. 1) is given off from the lateral side of the vestibular division. Immediately after its origin this canal takes an antero-ventral direction and crosses the proximal part of the canal sel_4 on the ventral side, continuing antero-laterally within the visceral endoskeleton, laterally to the otic region. In the *Cephalaspis*-species (text-fig. 13) it is generally rather short, opening with its anterior orifice high up in the roof of the oralo-branchial chamber. In *Kiaeraspis*, on the contrary, (text-figs. 4, 28, 36; pls. 49, 50, 51) it is much longer and has its anterior orifice far laterally in the roof of the oralo-branchial chamber, close medially to the third interbranchial septum and thus in the lateral part of the fourth branchial fossa.

Sinse the canal, IX *a*, now described does not branch like a canal for a vessel and since it is undoubtedly the only serial homologue of the canal which transmitted the most anterior branchial ramus from the vagus and in addition follows next anteriorly to that, it is beyond question that it transmitted the n. glossopharyngeus, after this nerve had traversed the postero-lateral part of the vestibular division of the labyrinth cavity. That this is the case is further, as we shall find, proved by the course and positions of the canals for the n. facialis and the canals for the trigeminus branches (cf. the chapter on the visceral endoskeleton).

More or less close dorso-medially or postero-dorso-medially to the interspace between the canals sel_1 and sel_4 one or a few canals always issue from the lateral portion of the vestibular division of the labyrinth cavity. I shall first describe these canals in *Cephalaspis hoeli*, then in certain other *Cephalaspis*-species and finally in *Kiaeraspis*.

In the specimen of *C. hoeli* used for section series A (text-figs. 18 A, B, C, D; 23, 25; section series A, nos. 64—84) a rather thick canal, *at*, leaves the vestibular division of the labyrinth cavity just dorso-medially to the interspace between the canals sel_3 and sel_4 and goes dorsally and somewhat anteriorly, soon joining two other canals *bt* and *ct*, which issue close to it likewise from the vestibular division. More exactly the former, *bt*, of the two last-mentioned canals, which is somewhat narrower than *at*, is given off from the vestibular division postero-dorso-medially to *at*, while the other one, *ct*, which is very fine, ascends from the vestibular division close antero-dorso-medially to *at*. On the left side of the specimen a fourth rather fine canal goes out from the vestibular division close posteriorly to *bt* and postero-dorsally to *at* (text-figs. 23, 25), and takes a dorso-lateral course to the most lateral part of the upper surface of the region. And on account of its mode of branching it is very likely that this canal transmitted a vessel, a vessel which must have been an artery, since, as has been pointed out, all the veins of this part of the region went dorsally and emptied directly or indirectly into the v. capitis lateralis. Besides this artery the canal in question may, however, have transmitted a fine dorsal branch from the n. facialis, a branch which may either have consisted of general cutaneous or lateralis fibres or of both. The common wide canal arisen by the union of the canals *at*, *bt* and *ct* soon divides into two branches, an anterior and a latero-superficial one.

The former of these branches is a rather wide, more or less distinctly circular canal, lettered in the figures VII (text-fig. 23—25; section series A, nos. 77—110), which goes forward and slightly latero-ventrally close beneath the dorsal surface of the otic region, crossing during its further course forward the canal sel_3 on the dorsal side under a very acute angle and being, during this part of its course, in open communication with that canal for a long distance. Finally, after having definitely arrived on the dorso-medial side of the canal sel_3 it becomes again independent of that and continues its further course a certain distance into the interspace between that and the canal $sel_{1,2}$, at last turning deeper down and opening with its distal opening into the oralo-branchial chamber. The canal VII, which thus from the vestibular division of the labyrinth cavity passes antero-latero-ventrally through the visceral endoskeleton, is, as we shall see, serially homologous with the canal IX *a* and the canal X_{br_1}; and as it follows immediately anteriorly to IX *a* it must evidently have been traversed by the n. facialis; and it will therefore be termed the facialis canal.

The latero-superficial branch, *a. la* (section series A, nos. 74—85), soon arrives at the upper surface of the otic region, where it turns laterally and somewhat anteriorly and leaving the region continues on the dorsal (external) surface of the visceral endoskeleton. It branches in such a way that there can be no doubt that it must have transmitted a superficial vessel. Since the dorsolateral superficial veins from the lateral portions of the otic region and the adjacent portions of the visceral endoskeleton, as we have seen, all went up to and emptied into the vena capitis lateralis, the canal *a. la* now described must obviously have lodged a strong latero-superficially running artery. The branches of the canal *a. la* could not be traced in detail in the specimen. On the other hand, as is shown by text-figs. 19, 23 and 25, it is fully clear that it communicated for a certain distance with the canal *v.* ls_4, i. e. with a vein canal.

In the specimen of *C. hoeli* from which section series B was made the conditions seem, as a whole to have been almost similar to those just described, but they are not as completely known as those (section series B, nos. 20—25).

If next we turn to the specimen of *C. hoeli* from which section series C was made, there is in that only one canal leaving the vestibular division of the labyrinth cavity medially to the interspace between the canals sel_3 and sel_4. Since this canal cannot be compared exactly with the three which were found at the corresponding place in the specimen used for section series A, I have lettered it in the figures *a. sa* + VII. It divides rather soon into a facialis canal (VII, section series C, nos. 87—105) and a canal (*a. sa*) which must have transmitted a dorso-lateral superficial arterial trunk. And of these at least the facialis canal (VII) went exactly as in the other specimens, but it is, however, easier to see here how it opened into the oralo branchial chamber.

In the specimen of *Cephalaspis vogti* figured in pls. 25, 26 and text-figs. 47, 48 the facialis canal (VII) can be traced backwards to its very origin from the vestibular division; and it is quite clearly seen that it leaves this division anteriorly to, and wholly independently of, the canal *a. la* for the dorso-lateral superficial arterial trunk. Both the facialis canal and the canal for the dorso-lateral superficial arterial trunk thus issue from the vestibular division of the labyrinth cavity independently of each other, and accordingly the conditions are in this respect very different from those in *C. hoeli.* Moreover in the specimen in question of *C. vogti* it is very well shown that the canal *a. la* is a vascular canal, which can only have transmitted an artery. Finally, we also see in this specimen that the canal *a. la* laterally on the visceral endosketeton must have divided into two chief branches, lettered *a. sa* and *a.* sm_1, and that accordingly the dorso-lateral superficial arterial trunk lodged in it broke up into two dorso-lateral superficial arteries. From the mode of origin now described of the facialis canal and the canal *a. la* from the labyrinth cavity in *C. vogti* there seems to be reason to believe that in the specimen of *Cephalaspis hoeli* used for section series A the canal lettered *bt* had given passage to a dorso-lateral superficial arterial trunk which continued laterally through the canal *a. la*, while the canal *at* would have transmitted the n. facialis.

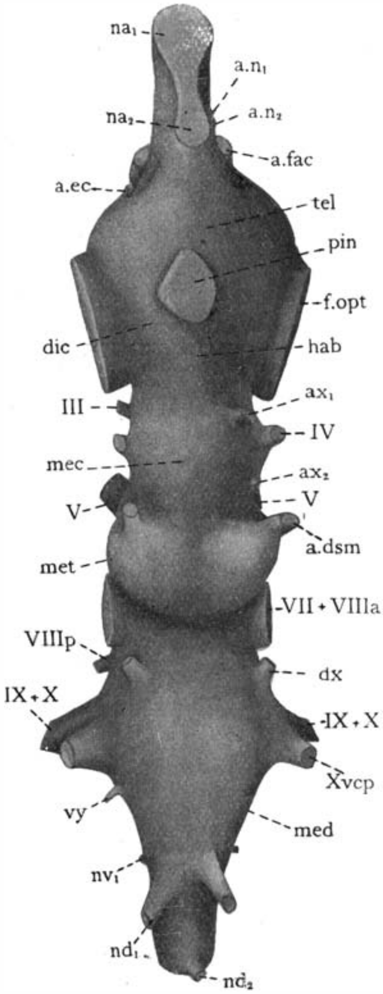
One specimen probably referable to *Cephalaspis heintzi* exhibits quite distinctly certain distal parts of the facialis canal (VII, pl. 29), which give off a rather considerable branch on the posterior side, a branch probably for a cutaneous nerve.

Finally in *Kiaeraspis* (text-figs. 19 A, B, C, D; 27; section series D, nos. 9—18; pls. 49, 50, 55) we find a fairly thick canal (VII + *a. sa*) issuing from the vestibular division of the labyrinth cavity rather high dorsally to the interspace between the canals *sel*$_3$ and *sel*$_4$. This canal leads antero-latero-ventrally to the visceral endoskeleton crossing the canal *sel*$_3$ on the dorsal side but, as far as can be seen, without anastomosing with that. When just above the canal *sel*$_3$ — at least in the specimen shown in pl. 55 — it gives off a branch on the posterior side, a branch, *a. sa*, which probably lodged a dorso-lateral superficial artery. Distally to that branch the canal (VII), which now seems to have been traversed only by the n. facialis, continues in the same direction as before, until it finally turns downwards and opens into the oralo-branchial chamber close dorso-medially to the interbranchial septum 2, that is, the interbranchial septum situated between the second and third branchial fossae (text-figs. 4, 36, pl. 51). As several fine branches are sent out from the distal parts of the canal, the n. facialis obviously, during that part of its course, supplied the portions of the visceral part of the shield in its surroundings.

In the specimen of *Kiaeraspis* from which section series D, was made there issues from the vestibular division of the labyrinth cavity close postero-dorsally to the canal just described a second but much thinner canal (*a. sm*$_1$, text-figs. 19 A—D, 27; section series D, nos. 15—18), which goes antero-laterally to the upper surface of the otic region and the adjacent part of the upper (lateral) surface of the visceral endoskeleton. This canal could not be traced to its end, nor could it be established whether it is a constant structure or not. As far as can be judged from what is known of it, it seems probable that it transmitted a small dorso-lateral superficial artery.

From what has been set forth concerning the n. facialis during and somewhat after its exit from the labyrinth cavity it is evident that, on leaving the labyrinth cavity and a certain distance distally to that, it was more or less closely accompanied by an arterial trunk for the superfical parts of the antero-lateral portions of the otic region and for the adjacent part of the external side of the visceral endoskeleton. We shall turn to this artery and its branches again below, after having dealt with the other arteries which issued from the labyrinth cavity. But before proceeding to that we shall consider a little more closely the nerves related to the labyrinth cavity.

It has already been pointed out above (pp. 86, 87) that the lateralis fibres which accompanied the n. trigemius and probably also the n. profundus entered the labyrinth cavity together with the roots of the n. facialis, quite as they do in the recent *Petromyzon*. And we thus find that all the lateralis fibres which associated with the prootic nerves went through the labyrinth cavity. The labyrinth cavity was, however, traversed not only by the lateralis fibres and by the n. facialis and the n. glossopharyngeus, but also by all or at least the majoritiy of the nerve fibres to the lateral



Text-fig. 20. *Kiaeraspis auchenaspidoides.* Cast of the cavum cerebrale cranii in dorsal view. After a model in wax made after section series D. Magnification about $^{20}/_{1}$.

a. dsm, canal for the postorbital superficial artery; *a. fac,* canal for the arteria facialis; *a.ec,* canal for a branch from the a. facialis to the cavum cerebrale cranii; $a.n_1$, and $a.n_2$, canals for branches from the a. facialis to the ethmoidal cavity. ax_1, ax_2 canals probably for arteries; *dic,* division of the cavum cerebrale for the diencephalon; *dx,* canal for an artery or a nerve to the posterior part of the dorsal electric field or for both an artery and a nerve; *f. opt,* optic fenestra; *hab,* bulge for the habenular ganglia; *mec,* division of the cavum cerebrale for the mesencephalon; *med,* division of the cavum cerebrale cranii for the medulla oblongata; *met,* division of the cavum cerebrale cranii for the metencephalon; na_1, external opening of the hypophysial sac; na_2, nasal opening proper; nd_1, canal for the myelonal vein 1 and probably also for the dorsal root of the spino-occipital nerve 1; nd_2, canal for the myelonal vein 2 and probably also for the dorsal root of the spino-occipital nerve 2; nv_1, canal for the myelonal artery 1, and probably for the ventral root of the spino-occipital nerve 1; *olf.c,* part of the ethmoidal cavity for the olfactory organ; *pin,* pineal opening; *tel,* division of the cavum cerebrale cranii for the telencephalon; *vy,* canal occuring only on the left side, probably for a vein; III, canal for the n. oculomotorius; IV, canal for the n. trochlearis; V, canal for the roots of the trigeminus and profundus ganglionic complex; VII+VIII*a*, canal for the n. facialis, for the electric fibres to the electric fields, for the prootic lateralis fibres and for the anterior branch of the n. acusticus; VIII *p*, canal for the posterior branch of the n. acusticus; IX+X, glossopharyngeus-vagus branch of the vagus canal; X*vcp*, branch of the vagus canal for the vena cerebralis posterior.

and dorsal electric fields. It is not quite excluded, of course, that a few of these nerve fibres for the most posterior part of the lateral electric field may have accompanied the n. glossopharyngeus to the labyrinth cavity and have had their exit from that through the canals sel_5 and sel_6, and that in addition certain nerve-fibres of the same kind, by means of the canal *dx*, may have gone up to the dorsal electric field. But there is no proof that it was so. And therefore it may also very well be possible that none of these fibres took these ways but that all passed through the acustico-facialis canal. In any case, however, it is quite clear that by far the greater part of them undoubtedly entered the labyrinth cavity through that canal which thus gave passage to the n. facialis proper (viscero-motor fibres, general cutaneous fibres and communis fibres), to all the prootic lateralis fibres, to all or at least to the vast majority of the nerve-fibres to the electric fields, and finally at least to the anterior branch of the n. acusticus.

The n. facialis and the lateralis fibres, which probably accompanied that nerve from the labyrinth cavity, seem to have had their ganglia on or rather close to the bottom of the vestibular division of the labyrinth cavity just as in *Petromyzon.* If the nerve fibres to the electric fields had any ganglionic formations these ganglionic formations were undoubtedly also situated in and close to the bottom of the vestibular division of the labyrinth cavity. And thus it is not improbable that the ventro-medial part of that divison of the labyrinth cavity was to a rather considerable extent occupied by ganglionic formations.

Immediately after their entrance into the labyrinth cavity, the lateralis fibres for the trigeminus and profundus nerves turned antero-laterally and went to the orbit through the canal *l.* A little further laterally (*Cephalaspis hoeli*) or approximately at the same place (*Kiaeraspis*) the electric fibres for the dorsal electric field separated from those for the lateral electric field and first took a dorsal course in the groove *dsv*, and then a dorso-medial course through the canal *des.* Somewhat further laterally the fibres for the lateral electric field were soon distributed into thick trunks, which were situated in the grooves on the bottom of the lateral and antero-lateral parts of the vestibular division of the labyrinth cavity, until they left the labyrinth cavity through the canals $sel_{1,2}$, sel_3, sel_4, sel_5, sel_6. The n. facialis during its passage through the labyrinth cavity was, at least in the lateral part of the vestibular division, situated dorsally to the nerves for the lateral electric field; and just when leaving the labyrinth cavity it must have turned rather straight dorsally. The n. glossopharyngeus obviously traversed only the postero-lateral part of the vestibular division of the labyrinth cavity and seems, at least most posteriorly, to have gone dorsally to the nerves for the lateral electric field. When leaving the labyrinth cavity, it took a more ventral direction, and just laterally to that cavity it crossed the canal sel_4 on the ventral side.

There are still a couple of canals issuing from the labyrinth cavity that have not yet been dealt with. For the study of these canals we shall, as in the case of the facialis canal and the arterial canal or canals related to this, first turn to the specimen of *C. hoeli* used for section series A.

In that specimen there issue two canals, lettered in the figures *dt* and *et*, from the postero-dorso-lateral part of the vestibular division of the labyrinth cavity (text-figs. 18 A—D; 23, 25, 26; section series A, nos. 57—70). More exactly the anterior one of these two canal, *dt*, leaves the vestibular division above the most proximal part of the canal sel_5 and takes a postero-lateral course, whereas the other one, *et*, goes out from the same division of the labyrinth cavity above the posterior part of the canal sel_6 and turns laterally, meeting and joining the anterior one in a common rather wide canal *a. slcm*, which runs laterally and slightly posteriorly first dorsally to the canal sel_6, soon, however, ariving at the dorsal surface of the visceral endoskeleton between that canal and sel_5.

In the specimen of *C. hoeli* used for section series B (nos. 6—10), as well as in the specimen of the same species figured in pls. 17 and 18, the canals *dt* and *ct* are present and appear to have united distally, exactly as in the specimen used for section series A. Similar or substantially similar conditions occur also in the specimens known in detail of *C. vogti* (text-figs. 47, 48, pl. 25), *C. heintzi* (text-fig. 46, pls. 29, 30) and *C. spitsbergensis* (text-fig. 49; pl. 39); and in these species it is also easy to follow the common canal *a. slcm* distally on the dorsal (external) side of the visceral endoskeleton and to observe that it divides into two main branches $a.\,sm_2$ and *a. sp*, and that it must be a vascular canal. Moreover it is also seen in those specimens, as, for instance, in that of *C. vogti* (text-fig. 48, pl. 25), that the vessel transmitted by the canal *a. slcm* and its branches $a.\,sm_2$ and *a. sp* must have been an arterial trunk which distally divided into two chief branches. And thus we find that this anterial trunk, like the anterior one or the two anterior ones which went more or less closely associated with the n. facialis, was a dorso-lateral superficial arterial trunk. Whether this superficial arterial trunk arose by the confluence of two arteries one of which traversed the canal *dt* and the other *ct* it is impossible to decide with full certainty from the conditions now considered, but it seems very likely that it was so.

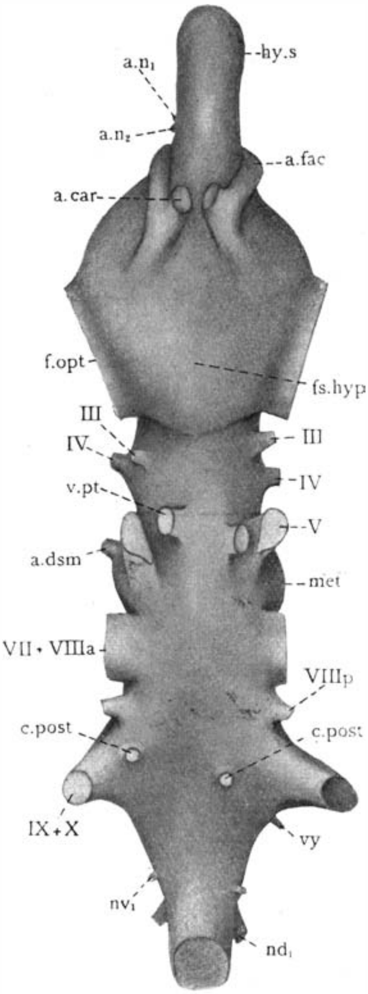
In the specimen of *C. hoeli* from which section-series C was made the conditions with regard to the canals from the postero-dorso-lateral part of the labyrinth cavity are rather different from those which have just been described. In that specimen also there are two canals which leave the postero-dorso-lateral part of the vestibular division of the labyrinth cavity (section series C, nos. 81—110); but these two canals do not unite with each other and accordingly they continue indepently of each other to the dorsal (external) surface of the visceral endoskeleton. The anterior one of these canals — which is lettered in the figures *a. sm* (section series C, nos. 95—108) — has its origin from the vestibular division dorsally to the canal sel_5 and goes antero-laterally, while the posterior one of them, which is denoted in the figures by the letters *a. sp* (section-series C, nos. 81—107), goes out from the same division of the labyrinth cavity postero-medially to the canal sel_6, taking a more straight lateral course. Both of them were undoubtedly arterial canals and the artery transmitted by the posterior one of them was certainly homologous with the artery transmitted through the canal *et* of the other specimens dealt with of *C. hoeli.* On the other hand, the artery which was lodged in the anterior one must probably have had a partial homologue in the other specimens of *C. hoeli* dealt with in an artery which was lodged in the canal *dt*; and thus we see that there is much reason to believe that this canal was an arterial canal too.

Finally, in the specimen of *Kiaeraspis* from which section series D was made there are two canals $a.\ sm_2$ and *a. sp*, (text-fig. 19, 27; section series D, nos. 1—10), which leave the vestibular division of the labyrinth cavity and pass off to the dorsal (external) surface of the visceral endoskeleton almost exactly as the canals *a. sm* and *a. sp* in the specimen of *C. hoeli* used for section series C. In *Kiaeraspis*, therefore, the posterior dorso-lateral arterial trunks must evidently have been developed much in the same way as in the specimen just quoted of *C. hoeli.*

The description given of the canals issuing from the labyrinth cavity has thus shown that several dorso-lateral superficial arterial trunks passed off from the labyrinth cavity to the dorsal (lateral) surface of the part of the visceral endoskeleton situated laterally to the otic region. As we shall see from the account given below, these dorso-lateral superficial arteries were not less than four, which, according to their position from in front backwards, may be called the dorso-lateral superficial arteries 1—4. Usually, as we shall see, these arteries have proximally at or just after their exit from the labyrinth cavity joined into two or three trunks. Thus in certain cases the dorso-lateral superficial artery 3 has united with the dorso-lateral superficial artery 4, and the dorso-lateral superficial artery 2 with the dorso-lateral superficial artery 1. In other cases, on the contrary, the dorso-lateral superficial arteries 2 and 3 joined each other. And finally in certain cases either the dorso-lateral superficial arteries 1 and 2 or the dorso-lateral superficial arteries 3 and 4. could have joined, while the other two remained independent. If we take these variations into account, it is, as we shall find, not difficult to understand the different conditions described here in the canals through which the arteries in question left the labyrinth cavity.

Below in the chapter on the blood vascular system, and in the chapter on the Cyclostomes, the homologues of the dorso-lateral superficial arteries will be discussed.

Orbitotemporal region. Like the otic region the orbitotemporal region, is indistinctly bounded externally both from the adjacent regions and from the visceral endoskeleton, with which it is continuous laterally (text-figs. 3—5, 7, 8, 13; section series A nos. 78—141; section series B, nos. 26—56; section series C, nos. 1—101; section series D; pls. 13, 14, 17, 19, 21, 23; pl. 24, fig. 2; pls. 28, 29, 44, 45, 48, 49, 50, 52—58). Since



Tezt-fig. 21. *Kiaeraspis auchenaspidoides.* Cast of the cavum cerebrale cranii in ventral view. From a model in wax made after section series D. Magnification $^{20}/_{1}$.

a. car, canal for the carotid artery; *a. dsm*, canal for the postorbital superficial artery; *a. fac*, canal for the arteria facialis; $a.n_1$, $a.n_2$, canals for branches from the a. facialis to the ethmoidal cavity; *c. post*, canal for the occipital encephalic artery; *fs. hyp*, hypophysial fossa, which most ventrally probably lodged also the posterior parts of the hypophysial sac; *f. opt*, optic fenestra; *hy. s*, division of the ethmoidal cavity for the hypophysial sac; nd_1, canal for the first myelonal vein and probably also for the dorsal root of the first spino-occipital nerve; nv_1, canal for the myelonal artery 1 and probably also for the ventral root of spino-occipital nerve 1; *v. pt*, canal probably for the pituitary vein; *vy*, canal occurring only on the left side, probably for a vein; III, canal for the n. occulomotorius; IV, canal for the n. trochlearis; V, canal for the roots of the trigeminus and profundus nerves; VII + VIII *a*, canal for the n. facialis, for the electric fibres to the electric fields, for the prootic lateralis fibres and for the anterior branch of the n. acusticus; VIII *p*, canal for the posterior branch of the n. acusticus; IX + X, glossopharyngeus-vagus branch of the vagus canal.

the trigeminus roots pierced the cranial wall rather far back behind the dorsum sellae and thus above the parachordal part of the neurocranium, the region evidently extended farther back with its dorso-medial than with its ventro-medial parts. Forwards, on the other hand, it seems to have reached less far with its dorso-medial than with its ventro-medial parts.

Roughly speaking, the length of the region may be considered to be equal to the length of the orbits, and, as is seen from the figures, the length is always much less than the breadth, being as a rule only about a third or less as large. Its height, except perhaps in the most medial parts, is regularly somewhat less than that of the otic region.

The orbits, which fall within the region, as usually, are bounded on the medial, ventral and partly also on the lateral side by the region. Since they have a complete posterior wall which, as we have seen, is constituted by the otic region and an anterior wall formed by the ethmoidal region we may be justified in considering that there is here a complete optic capsule. As far as can be judged, this peculiar condition seems, at least to a certain degree, to be a secondary character caused by the shifting of the orbits from an originally lateral position, about as in Pteraspids, to the present position close to each other on the dorsal side of the head.

Apart from the orbital surfaces the region has only two external surfaces, a dorsal one and a ventral one both of which are continuous with the corresponding surfaces of the adjacent regions and also with the correspondingly situated surfaces of the visceral endoskeleton.

The dorsal surface (text-figs. 2, 7, 8; section series A, nos. 78—141; section series B, nos. 26—56; section series C, nos. 1—101; pls. 17, 18, 29, 39), like that of the otic region, is as a whole more or less strongly convex, with the median interorbital part flattened. On these flattened median part opens the pineal canal (*pin*, text-figs. 3, 15, 17, 20, 22, 23, 25, 27; and in a great number of the plates). Immediately behind that lies the most anterior part of the dorsal electric field (*dsf*), which thus reaches rather far forward on the region. Somewhat laterally to the pineal opening, and to the anterior part of the dorsal electric field, we find the orbital opening which, as it lies on the laterally sloping part of the dorsol surface, always faces not only dorsally but also laterally. In addition the orbital opening may rather often be directed so that it also faces slightly anteriorly. For other details concerning the shape etc. of the orbital opening the reader'is referred to p. 21 above.

The ventral surface (text-figs. 4, 13; section series A nos. 78—141; section series B, nos. 26—56; section series C, nos. 1—101; pls. 14, 20; pl. 26; pl. 33, figs. 1; pl. 44; pl. 46, fig. 1; pls. 51—58 is lined by the external perichondral bone layer and forms part of the upper surface of the oralo-branchial chamber. It is limited posteriorly by the orbito-otical groove (*orb. ot. gr*), anteriorly by the bottom of the subnasal fossa (*f. sn.*). On its medial part we find the more or less high aortal ridge (*r. aort*) with its goove — the aortal groove (*aort. gr*). And on each side of that ridge the orbital prominence (*pr. orb*), a bulge caused by the orbit, is distinctly seen. At least in certain forms, such as *Hoelaspis* (pl. 44; pl. 46, fig. 1) and *Kiaeraspis*, there is on the anterior part of each orbital prominence a delicate transverse ridge which goes to the aortal ridge, and which, at least in the vicinity of that, is grooved in its longitudinal direction. This ridge (*a. eff*$_3$) is the dorsal part of the interbranchial ridge 3, and its groove must certainly have been developed for an efferent gill artery, which, as we shall see, was the third one, counted from in front. From the aortal groove a paired canal (*a. car*) leads upwards into the region close behind the transition to the ethmoidal region. That this canal lodged an artery is easy to conclude, and, as we shall see, that artery was the carotid artery.

The part of the region situated between the orbits — the interorbital wall, as it will be termed in the subsequent account — is thick and strong (text-figs. 23—28; section series A, nos. 78—141; section series B, nos. 26—56; section series C, nos. 1—101; section series D; pls. 14, 15; pl. 19, fig. 1; pls. 21, 28, 45; pl. 47, fig. 1; pls. 48, 49, 55); and the cavum cerebrale cranii extends forwards through it in its entire length.

The orbit of each side (*orb*, text-figs. 23—28; section series A, nos. 78—141; section series B, nos. 26—56; section series C, nos. 41—89; section series D; pls. 14, 15, 18; pl. 19, fig. 1; pls. 21, 28, 45, 48, 49, 50) is a large space, which is always longer than it is broad and at least in certain forms almost as deep as it is long. As has already been pointed out, it is lined throughout by a perichondral bone-layer of its own — the orbital bone-layer — which is directly continuous with the inner bone-layer and with the exoskeleton and by means of canal-layers with the external bone-layer. In addition it is also by means of canal-layers continuous with both the internal bone-layer and the exoskeleton.

In the fossil state there is a very wide fenestra between the orbit and the part of the cavum cerebrale situated in the interorbital wall. This fenestra (*f. opt,* text-figs. 15—17, 20—24, 27, 28; section series A, nos. 100—123; section series B, nos. 39—46; section series C, nos. 37—48; section series D, nos. 2—25), through which, as we shall see, the n. opticus had its exit and which may therefore be called the optic fenestra, is known in detail only in *Cephalaspis hoeli* and in *Kiaeraspis.* As is seen from the figures cited it is relatively bigger in the former than in the latter. In both it has a triangular shape, with the angles rounded off, but while in *C. hoeli* the anterior angle is usually the most acute one we find instead in *Kiaeraspis* that the posterior angle is more acute than the others. In the Cephalaspids when alive, the optic fenestra was certainly closed by a more or less thick membrane, a membrane formed at least partly by the dural connective tissue.

At its postero-ventro-medial part, close to the bottom, the orbit is continuous with a wide canal (*my*, text-figs. 23, 24, 27, 28; section series A, nos. 86—98; section series B, nos. 29—38; section series C, nos. 1—60; section series D, nos. 4—20; pls. 8, 14; pl. 19, fig. 1; pl. 23, fig. 1; pls. 25, 26, 45, 48, 49, 55), which penetrates medially and, at least in certain cases, somewhat posteriorly into the ventral wall of the neurocranium slightly behind the dorsum sellae and thus in the parachordal division of the endocranium. In all forms this canal diminishes in diameter medially, and mostly it seems to end blindly in the vicinity of the median line close to its fellow of the oposite side. But in certain cases —

as for instance in the specimen of *Cephalaspis hoeli* shown in section series B (nos. 37, 38)[1] — it was connected with and opened into that of the opposite side, so that in this specimen the orbits were in communication with each other posteriorly in the postero-ventral part of the otic region. As is well shown, the two canals of the specimen just referred to meet and join each other close above the notochord, which so far forward as this began to turn upwards from its superficial position on the ventral side of the ventral cranial wall and to penetrate into the dorsum sellae. In a second specimen of *C. hoeli* — that from which section series C was made — they certainly came very close to each other with their medial ends, but whether they communicated with each other or not could not be be ascertained, since the orbital bone-layer which lines them was not well preserved most medially. As in a third specimen of *C. hoeli* — the one used for section series A — they end blindly rather far from each other, it is obvious that their medial extension is subject to rather great variations even in different specimens of the same species.

From the relatively very considerable size of the orbit we are of course justified in concluding that the eye was large and well developed. And under these conditions it is evident that its recti muscles must have been strong and large too, so that at least certain of them required an enlarged area of origin and that owing to this the canal *my* described just above was formed by their most postero-dorsally extending parts. Accordingly, if I am right, this canal would represent a myodome.

The canal *my* which therefore in the account below will be referred to as the myodome, is, when it meets and communicates with its fellow of the opposite side in the median line, evidently equivalent to an anterior portion of the prootic part of the myodon of *Amia* (cf. ALLIS 1897, pp. 492—506, 516—519; 1903 b, pp. 93—95; 1914, pp. 246—248; 1918 a, pp. 241—246; 1919, pp. 264—271; STENSIÖ 1925 a, pp. 55—57), to a little more than the prootic part of the myodome of *Birgeria* (STENSIÖ 1921, pp. 162—175; 177—180; 1925 a, pp. 62—64; ALLIS 1922 a), approximately to the myodome of *Saurichthys* (STENSIÖ 1925 a, pp. 52—73) and to an anterior portion of the prootic part of the dorsal compartment of the normal Teleostean myodome (cf. SAGEMEHL 1885, pp. 85—87; 1891, pp. 574—576; ALLIS 1903 b, pp. 91—95; 1909 a, pp. 44—45, 145, 183—208; 1914, pp. 225—251; 1918 a, pp. 241—246; 1919, pp. 207—264). It is highly probable that it has arisen in the Cephalaspids after these had differentiated as a separate group of Ostracoderms. In this connection it may also be worthy of notice that the myodome of fishes must have arisen independently in different groups (cf. STENSIÖ, 1925 a).

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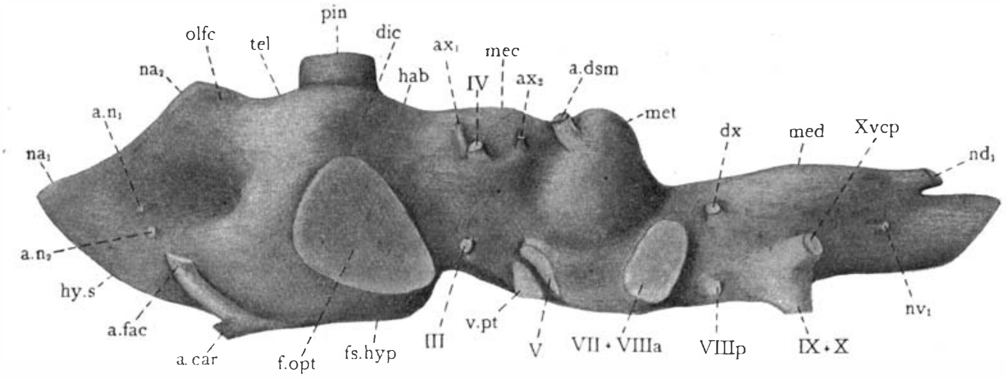
[1] cf. also pl. 19, fig. 1 and pl. 14.



Text-fig. 22. *Kiaeraspis auchenaspidoides.* Cast of the cavum cerebrale cranii in lateral view. Model made in wax after section series D. Magnification $^{20}/_{1}$.

a. car, canal for the carotid artery; *a. dsm,* canal for the postorbital superfical artery; *a.fac,* canal for the arteria facialis; $a.\ n_1$, $a.\ n_2$, canals for fine arterial branches to the hypophysial sac; ax_1, ax_2, fine canals probably for arteries; *dic,* division of the cavum cerebrale for the diencephalon; *dx,* canal for an artery or a nerve to the posterior part of the dorsal electric field or for both an artery and a nerve; *f. opt,* optic fenestra; *fs. hyp,* hypophysial fossa, which most ventraly probably lodged also the posterior parts of the hypophysial sac; *hab,* faint bulge for the habenular ganglia; *hy. s,* division of the ethmoidal cavity for the hypophyseal sac; *mec,* division of the cavum cerebrale cranii for the mesencephalon; *med,* division of the cavum cerebrale for the medulla oblongata; *met,* division of the cavum cerebrale for the cerebellum; na_1, external opening of the hypohpyseal sac; na_2, nasal opening proper; nd_1, canal for the myelonal vein 1 and probably also for the dorsal root of the spino-occipital nerve 1; nv_1, canal for the myelonal artery 1 and probably also for the ventral root of spino-occipital nerve 1; *olf. c,* part of the ethmoidal cavity for the olfactory organ; *pin,* canal for the pineal organ; *tel,* division of the cavum cerebrale cranii for the telencephalon; *v. pt,* canal probably for the pituitary vein; III, canal for the n. occulomotorius; IV, canal for the n. trochlearis; V, canal for the roots of the n. trigeminus and the n. profundus; VII+VIII *a,* canal for the n. facialis, for the electric fibres to the electric fields, for the prootic lateralis fibres and for the anterior branch of the n. acusticus; VIII *p,* canal for the posterior branch of the n. acusticus; IX+X, glossopharyngeus-vagus branch of the vagus canal; X*vcp,* branch of the vagus canal for the vena cerebralis posterior.

On account of its relation to the roots of the trigeminus ganglionic complex the myodome of the Cephalaspids, besides the division already described, also, as we shall see, has a small dorso-postero-lateral division, which corresponds to a small portion of the trigeminus part of trigemino-facialis chamber of fishes.

The division of the cavum cerebrale cranii falling within the region (text-figs. 2, 15—17, 20—28; section series A, nos. 78—131; section series B, nos. 27—48; section series C, nos. 1—38; section series D, nos. 1—34; pls. 13, 14; pl. 19, fig. 1, pls. 21, 28, 45; pl. 47, fig. 1; pls. 48, 49, 55) is most posteriorly rather high but comparatively narrow. Immediately anteriorly to the dorsum sellae, however, it suddenly becomes still higher and often also broader than posteriorly, attaining its greatest dimensions approximately between the posterior parts of the middle halves of the orbits. Here, in fact, we have always the highest and in certain forms, as for instance *Kiaeraspis*, the widest part too of the whole cavum cerebrale cranii. The ventral portion of the anterior wide and high part of the division forms a long and broad fossa hypophyseos (*fs. hyp*).

For the further description we may consider the region to be composed of a ventral and a dorsal wall both of which are unpaired, and a lateral wall which is paired (section series A, nos. 78—141; section series B, nos. 26—56; section series C, nos. 1—101; section series D). The ventral wall which anteriorly, just at the anterior end of the fossa hypophyseos passes over into the ventral wall of the ethmoidal region, reaches backwards only to the dorsum sellae. As a whole it is broad and thin; and on each side laterally to the interorbital wall it forms the floor and in addition most laterally, where it is somewhat thickened, a low lateral boundary for the orbit. Somewhat laterally to the orbit it merges into the visceral endoskeleton. The dorsal wall, which extends further backwards but not quite as far forwards as the ventral one, is thicker but much narrower than that. Laterally it overhangs the orbit of each side so that in fact it forms also a roof for this. On the upper side of its posterior parts we find the most anterior portion of the dorsal electric field. Finally, the lateral wall of each side forms the septum between the orbit and the part of the cavum cerebrale falling within the region. Posteriorly this wall extends further backwards with its dorsal than with its ventral parts, while anteriorly, on the contrary, it exhibits reverse conditions, i. e. it there reaches farther forwards with its ventral than with its dorsal parts.

After this description of the general features of the region we shall turn to its canals beginning with those which issue from the cavum cerebrale cranii. These have been studied in detail in *Cephalaspis hoeli* and in *Kiaeraspis*.

In *Cephalaspis hoeli* we find regularly a rather wide canal, V*d*, (text-figs. 16, 17, 24; section series A, nos. 70—83; section series B, nos. 19—29; section series C, nos. 1—9; 33—41; pl. 18; pl. 19, fig. 1; pl. 23, fig. 3) which leaves the bottom of the cavum cerebrale cranii close medially or immediately antero-medially to the acustico-facialis canal and which goes forwards and slightly laterally to the postero-lateral part of the myodome, opening into that with an often somewhat widened anterior opening. As is seen from the section figures, this canal begins most posteriorly as a shallow groove on the bottom of the cavum cerebrale close antero-medially to the acustico-facialis canal, a groove which rapidly deepens forwards and soon becomes transformed into a canal. Most posteriorly the canal lies close beneath, further forwards close ventro-laterally to the cavum cerebrale cranii. It is evidently throughout its entire length situated within the parachordal division of the skull; and thus it pertains really to the otic region, but, as we shall see, it was for practical reasons necessary to describe it in this connection. Rather close anteriorly to its posterior opening a fine canal (V_x, text-fig. 17; section series A, nos. 74—77; section series B, nos. 23, 24) leads ventro-laterally to it from the cavum cerebrale cranii, and towards its anterior end it is by a second fine canal (V_{xa}, text-fig. 16; section series A, nos. 81—87; section series B, nos. 24—27; section series C, nos. 27—29) also in communication with the cavum cerebrale cranii.

Slightly dorsally to the middle of the canal V*d* just described a second somewhat finer canal, *Vc* (text-figs. 16—17; section series A, nos. 80—83; section series B, nos. 28, 29; section series C, nos. 36—48), issues in *C. hoeli* from the cavum cerebrale forwards, downwards and slightly laterally through the lateral wall of the otic region and perhaps also through the most posterior part of the lateral wall of the orbito-temporal region. This canal goes to the myodome too, opening into that immediately dorsally to or even partly together with V*d*. Behind its origin from the cavum cerebrale it is continued by a distinct groove (text-fig. 17; section series A, nos. 73—80) which leads backwards in a direction towards the dorsal part of the internal opening of the acustico-facialis canal. From the course of this groove we are justified in concluding that the structure which had its exit through the canal V*c* must have had a rather long intra-cranial course and have arisen from the brain somewhere in the vicinity of the dorsal part of the acustico-facialis canal. Finally it is also noteworthy that the canal V*c*, after its opening into the myodome, is continued on the posterior side of that for a certain distance laterally by a distinct groove which in places is bridged over anteriorly and which thus in places is transformed into a completely closed canal (section series C, nos. 43—49). Owing to this it is easy to see that the structure which traversed it went out to the postero-ventro-medial part of the orbit.

Somewhat dorsally and slightly anteriorly to the canal V*c* a third canal (text-figs. 15—17, 23; section series A, nos. 80—92; section series B, nos. 30—38) goes, in *C. hoeli*, out from the cavum cerebrale cranii in an anterior and slightly lateral direction. In fact this canal — which, as may be seen from the figures, is situated rather high — perforated the most postero-lateral part of the lateral wall of the region. Very soon after its origin it divides into a dorsal and a ventral branch. The former of these two branches, IV, which usually is the narrower of the two, takes an antero-latero-dorsal course to the postero-dorso-medial part of the orbit. The ventral branch, which is lettered V*b* in the figures, on the contrary, turns ventrally and somewhat antero-laterally and goes to the myodome into which it opens on the dorsal side close medially to or just at the transition to the orbit.

Not far antero-ventro-medially from the point at which the two branches IV and V*b* separate we find, in *C. hoeli*, a fourth canal issuing from the cavum cerebrale cranii. That canal, V*a* (text-figs. 16—17; section series A, nos. 90—92; section series B, nos. 33, 34), which seems to be rather fine, may either go ventrally and slightly antero-laterally through the lateral wall of the region to the medial part of the myodome half of its side, opening independently into that from the dorsal side or else it may take a more straight lateral course, opening into the myodome together with the canal *Vb*.

Ventrally or slightly anteriorly to the canal *Vb* there is, in *C. hoeli*, a short and rather fine canal, *v. pt* (text-figs. 16, 17, 24; section series A, nos. 88—94; section series B, nos. 36—38), which on each side leads from the bottom of the cavum cerebrale cranii ventro-laterally through the ventral wall of the otic region somewhat behind the dorsum sellae to the medial part of the myodome half of its side. In the specimen from which section series C was made only faint traces of this canal could be observed, a condition which, however, may be due to the imperfect state of preservation in which the medial parts of the myodome were found there.

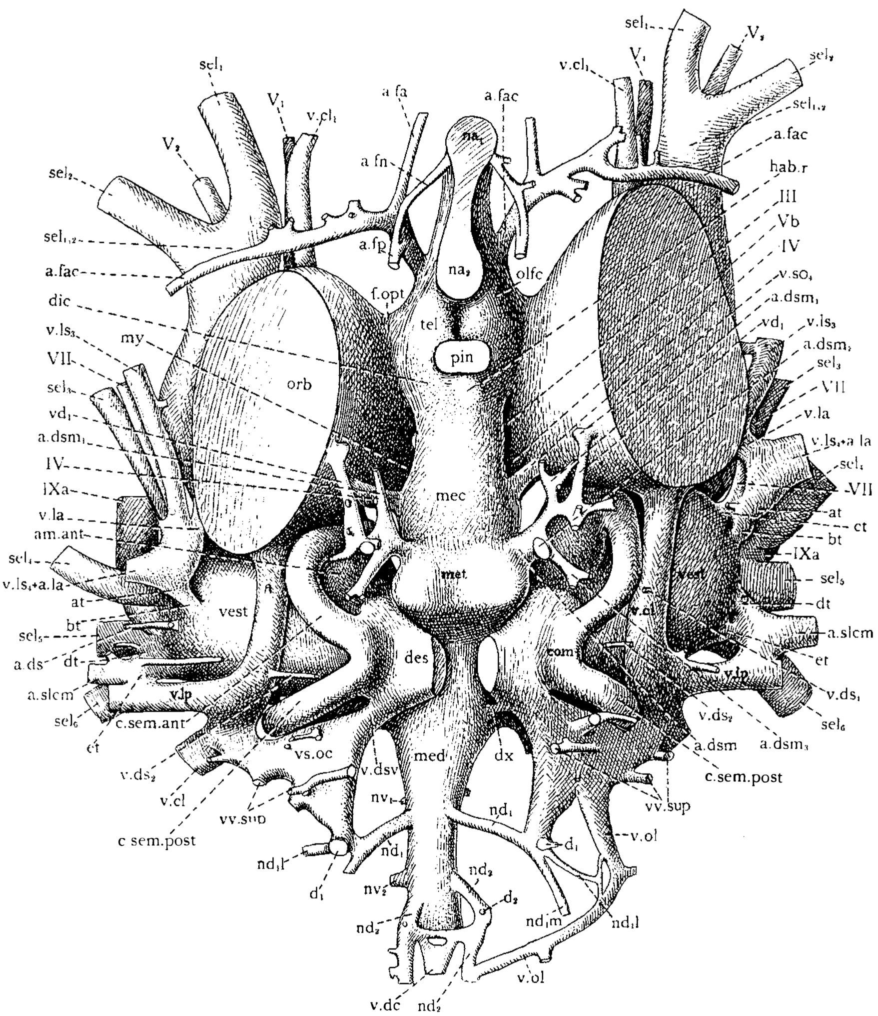
The canal which, in *C. hoeli*, leaves the cavum cerebrale cranii next in front of *v. pt* is a rather fine one, III (text-figs. 15—17, 23; section series A, nos. 96—100; section series C, nos. 31—35), which lies higher than *v. pt*, immediately behind the optic fenestra and, as is seen from the figures, almost straight above the dorsum sellae. Its internal opening is situated rather high above the bottom of the cavum cerebrale. The canal pierces the lateral wall of the region in a lateral and somewhat antero-ventral direction, opening into the orbit either in the very posterior margin of the fenestra optica, as in the specimen used for section series C (nos. 31—35), or very close behind that. Accordingly it reached the orbit rather far antero-ventrally to the canal IV.

From its course and position as here described it is very easy to conclude that the canal III must have been traversed by the n. occulomotorius (cf. AHLBORN 1883, pl. 13, fig. 2; 1884, pl. 18, fig. 6; JOHNSTON 1902, pl. 1, fig. 1; HERRICK & OBENCHAIN 1913, fig. 2; etc.) and that this nerve went exactly as in recent Petromyzontids (cf. text-figs. 29, 30, 32).

Of the other canals treated here in *C. hoeli* the one lettered *v. pt* might, of course, owing to the fact at it goes out from the very bottom of the cavum cerebrale, be thought to have transmitted the n. abducens. But if we take into account its transverse direction in relation to the longitudinal axis of the cavum cerebrale it seems hardly probable that it gave passage to that nerve, which, as we shall see, if it was present, instead probably accompanied one of the trigeminus roots through the cranial wall. On the contrary, I am inclined to believe that it was 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. As far as can be judged, this vein seems thus with regard to its position within the cranial basis, with regard to its relations to the myodome and with regard to its function to have been at least partly homologous to the pituitary vein of fishes (cf. GEGENBAUR 1872, pp. 75—79; SAGEMEHL, 1884, pp. 215—217; 1885, pp. 85—87; 1891, pp. 574—575; ALLIS 1897, pp. 492—497, 1903 b, pp. 91—95; 1909 a, pp. 43—51, 183—208; 1914, pp. 225—253; 1919; 1922 a; 1922 b, pp. 225—226; ALLEN 1905, p. 81, pl. 2, fig. 15; O'DONOGHUE 1914, pp. 440—441; LEHN, 1918, p. 364; STENSIÖ, 1921, pp. 62, 95, 164—165, 177—180; 1922, pp. 178—179; 1923, p. 1244; 1925 a, p. 54; DE BEER 1924; 1926, etc.). And accordingly it seems as if the myodome of the Cephalaspids, like that in fishes, had arisen by the invading of certain of the recti muscles of the eye into the canal for the pituitary vein.

In the description of the otic region (pp. 71, 72, 86, 87 above) it was pointed out that certain of the lateralis fibres, which accompanied the n. facialis to the labyrinth cavity, immediately after they had reached the vestibular division of that cavity must have turned anteriorly and slightly laterally and have gone to the orbit. As was also mentioned they reached the orbit through the canal *l*. This canal opens into the postero-ventro-medial part of the orbit close to the bottom and slightly laterally to the orbital opening of the myodome (text-figs. 24, 28; pl. 18; pl. 19, fig. 1; pl. 23, fig. 3); and on the bottom of the orbit it is continued for some distance antero-laterally by a groove (section series A, nos. 72—93; sectton series B, nos. 21—31; section series C, nos. 49—68). Under the assumption that it really had the function I have ascribed to it, and thus that the conditions with regard to the lateralis fibres which went forward to the orbit to associate with the trigeminus branches were almost exactly as in the recent *Petromyzon* (text-fig. 38; cf. also AHLBORN 1884, p. 300; JOHNSTON 1905, pp. 157—163), it is highly probable that these fibres, likewise just as in *Petromyzon*, did not become ganglionic until after their entrance into the orbit. Accordingly the ganglion of these lateralis fibres would, if I am right, have been situated on the bottom of the orbit close laterally to the orbital opening of the myodome.

The canals V*b*, V*c* and V*d* of *C. hoeli* unquestionably transmitted the n. trigeminus and the n. profundus. Since, however, they leave the cavum cerebrale not only at very different heights but also on very different transversal planes, it is fully clear that they cannot have given passage to the large trigeminus trunks and the n. profundus as such but instead to the roots of these nerves. And in fact, as we shall find from the account of the cavum cerebrale cranii given below, they show



Text-fig. 23 A. *Cephalaspis hoeli.* The cavum cerebrale, the labyrinth cavity the orbits and the canals related to these cavities. Dorsal aspect. The figures is drawn after a model in wax made after section series A. $^{10}/_{1}$.

a. ds, canal for a small dorso-lateral superficial artery; *a. dsm*, canal for the arteria superficialis postorbitalis; *a. dsm*$_1$, *a. dsm*$_2$, *a. dsm*$_3$, branches of the canal *a. dsm*; ***a. fa***, anterior branch of the canal for the facial artery; *a. fac*, canal for the facial artery; *a. fn*, canal for a branch of the facial artery to the hypophysial sac; *a. fp*, canal for a posterior branch of the facial artery; *a. la*, canal for a dorso-lateral superficial arterial

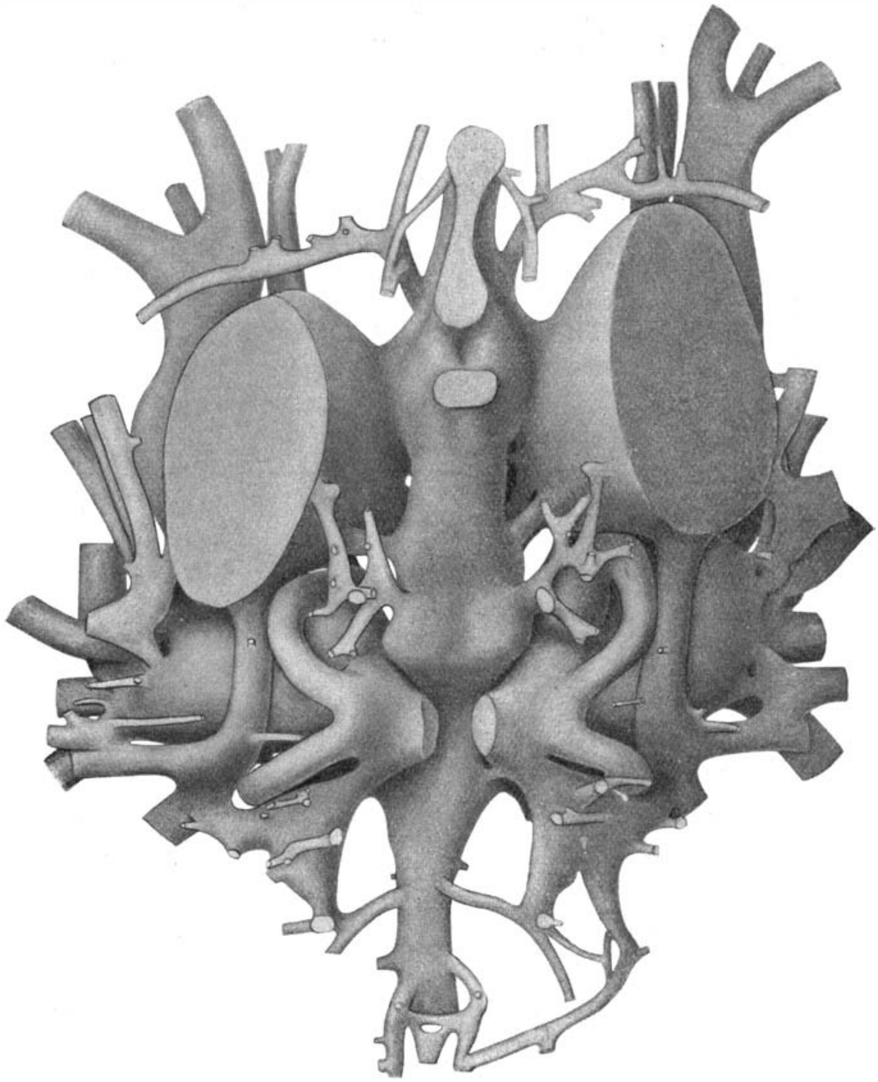
(Text-fig. 23 A. Continued.)

trunk arisen by the confluence of the two anterior dorso-lateral superficial arteries; *a. slcm*, canal for a dorso-lateral superficial arterial trunk arisen by the union of the two most posterior dorso-lateral superficial arteries; *am. ant*, swelling for the ampulla anterior; *am. post*, swelling for the ampulla posterior; *at, bt, ct*, canals for the n. facialis and for dorso-lateral superficial arteries; *com*, commissural division of the labyrinth cavity; *c. sem. ant*, division of the labyrinth cavity for the canalis semicircularis anterior; *c. sem. post*, division of the labyrinth cavity for the canalis semicircularis posterior; d_1, canal probably for the ductus endolymphaticus and in many cases also for a vein from the dorsal electric field; d_2, short canal probably for a vein from the dorsal electric field; *des*, canal for the electric nerve to the dorsal electric field. The canal probably transmitted also a vein from that electric field; *dic*, division of the cavum cerebrale for the diencephalon; *dt*, canal for an artery; *dx*, canal for a nerve or for an artery or for both; *et*, canal for an artery; *f. opt*, optic fenestra; *hab. r*, bulge indicating the position of the ganglion habenulæ. Note the asymmetrical development, indicating that the right ganglion habenulae was bigger and situated more posteriorly than the left one; *mec*, division of the cavum cerebrale for the mesencephalon; *med*, division of the cavum cerebrale for the medulla oblongata; *met*, division of the cavum cerebrale cranii for the metencephalon; *my*, myodome; na_1, opening of the hypophysial sac; na_2, nasal opening; nd_1, canal for the myelonal vein 1 and probably also for the dorsal root of the spino-occipital nerve 1; $nd_1\,l$, canal probably for a vein; nd_2, canal for the myelonal vein 2 and probably also for the spino-occipital nerve 2; $nd_1\,m$, medial branch of the canal nd_1, a branch which probably transmitted the dorsal root of the first spino-occipital nerve; nv_1, canal for the ventral root of spino-occipital nerve 1. In addition this canal transmitted the myelonal artery 1; nv_2, canal for the ventral root of the spino-occipital nerve 2. The canal gave also passage to the myelonal artery 2; *olf. c*, space which lodged the olfactory organ; *orb*, orbit; *pin*, pineal canal; sel_3--sel_6, canals for the electric nerves to the lateral electric field; $sel_{1,2}$, common canal for the first and second electric nerves to the lateral electric field; *tel*, division of the cavum cerebrale for the telencephalon. *v. cl*, canal for the vena capitis lateralis; $v.\,cl_1$, canal for the preorbital portion of the vena capitis lateralis; $v.\,d_1$, vein canal leading to the orbit; $v.\,ds_1$, $v.\,ds_2$, canals for veins from the dorsal parts of the otic region; *v. dsv*, canal for the otical vein. The ductus endolymphaticus probably reached backwards through this and d_1 to the upper surface of the neurocranium; *vest*, vestibular division of the labyrinth cavity; *v. la*, *v. lp*, canals for lateral tributaries to the vena capitis lateralis; $v.ls_3$, canal for the dorso-lateral superficial vein 3. $v.\,ls_4 + a.\,la$, common canal for the dorso-lateral superficial vein 4 and the anterior dorso-lateral superficial arterial trunk arisen by the union of the the anterior dorso-lateral superficial arteries; *v. ol*, canal for the lateral occipital vein; *vs. oc*, occipital vein sinus; *v. so*, canal for a vein from the dorsal side of the interorbital wall and the anterior part of the dorsal electric field; *vv. sup*, canals for superficial veins leading to the occipital vein sinus; IV, canal for the n. trochlearis; V b, canal for the general cutaneous root of the n. profundus (trigemini); V_1, canal for the n. profundus; V_2, canal for the n. trigeminus proper; VII, canal for the n. facialis from the labyrinth cavity; IX*a*, canal for the n. glossopharyngeus from the labyrinth cavity.

by their origins from the cavum cerebrale rather distinctly how the trigeminus and produndus roots issued from the medulla oblongata. We are thus able to establish here that the trigeminus-profundus ganglionic complex was situated externally to the canals V*b*, V*c*, and V*d*. And this having been the case, it is evident that it must have lain with a small part just distally to the openings of the canals V*b*, V*c*, and V*d* within the postero-lateral part of the myodome, but that the chief part of it was situated immediately antero-laterally to the myodome in the postero-ventro-medial part the orbit. With regard to its position it should further be added here that it certainly lay medially and morphologically anteriorly to the ganglion of the lateralis fibres, which entered the orbit through the canal *l*.

With the guidance of the knowledge we possess concerning the roots of the trigeminus-profundus ganglionic complex in recent fishes (KINGSBURY 1897; JOHNSTON 1898, fig. 12; 1901, p. 65, pl. 13; HERRICK 1899, pls. 15, 16; 1900, pp 269—270, 272, pl. 21; 1901, pp. 181—186, pls. 14, 15; ALLIS 1897, pp. 593—623, pl. 30, figs. 38, 39; 1901, pp. 144—150; 1903b, pp. 245—272; 1909a, pp. 80—83; 1922b, pp. 271—283; VEIT, 1911, pl. D, fig. 10; NORRIS & HUGHE 1920, pp. 320—355) and in recent Cyclostomes (AHLBORN 1883, pl. 13, fig. 2; 1884, p. 300; HATSCHEK 1892, fig. 11; v. KUPFER 1895; 1906; KOLTZOFF, 1901, pp. 333—381; JOHNSTON 1902, pp. 49—51; 1905, pp. 151—163; 1908; WORHINGTON 1905, pp. 164—172; NEYMAYER 1906; AYERS & WORTHINGTON 1908; HERRICK & OBENCHAIN 1913, fig. 2; HOLMGREN 1919) we are able to conclude with a great degree of probability which of the roots of the trigeminus ganglionic complex that emerged through each of the canals V*b*, V*c*, and V*d* described in *C. hoeli*.

We first turn to V*d*. On account of its origin from the cavum cerebrale cranii very low and far back, close medially to the acusticofacialis canal, it must have given passage either to the viscero-motor root V alone or to that root together with a bundle of communis fibres to certain of the trigeminus branches (cf. text-figs. 38, 42). Since, however, *C. hoeli* otherwise in many anatomical features appears to agree very well with the Cyclostomes, it seems probable that with regard to its trigeminus nerve too it was much more suggestive of the Cyclostomes than of fishes in general and that the communis fibres of that nerve therefore during the passage to the trigeminus ganglionic complex were closely associated with the general cutaneous fibres (AYERS & WORTHINGTON 1911). Accordingly, if I am right in this supposition, the canal V*d* would have transmitted only the viscero-motor root V. To judge from the width of the canal V*d* that root would have been thick and strong just as it is in the Cyclostomes (cf. AHLBORN 1884, pl. 18, fig. 5; JOHNSTON 1905, pl. 5; WORTHINGTON 1905, pl. 11; HOLMGREN 1919, text-fig. 27; cf. also text-figs. 38 and 42 in the present work).



Text-fig. 23 B. *Cephalaspis hoeli.* The cavum cerebrale, the labyrinth cavity, the orbits and the canals related to these cavities. Dorsal aspect. The figure is drawn after the same model in wax as text-fig. 23 A.

On account of its position and course in relation to the cavum cerebrale cranii and to the canals V*d* and V*b*, the canal V*c* must be considered to have given passage to the generai cutaneous root forming the ganglion gasseri and thus to the general cutaneous root of the trigeminus proper. As has been pointed out above, this root was probably accompanied by certain communis fibres, which were intimately associated with it.

Finally, the canal V*b* must have been traversed by fibres which left the antero-dorsal corner of the medulla; and it is therefore very easy to conclude that these fibres must have been general cutaneous ones and that they constituted the root which formed the profundus ganglion. Since the canal V*b* is comparatively wide there can be no doubt that the root which traversed it was thick too. With regard to its place of origin from the brain, with regard to its course and position and with regard to its considerable thickness that root must have resembled very closely the corresponding root in Cyclostomes. Probably, like that, it had communis fibres intimately associated with itself.

The canal IV, which, as we have found, issues from the cavum cerebrale together with the canal for the profundus root, must evidently have been traversed by the n. trochlearis. As is easily understood from its direction when it separates from the profundus canal, the n. trochlearis must, very soon after its entrance into the cranial wall, have crossed the profundus root on the dorsal side. And it deserves to be emphasized here that just at the crossing it was situated closely upon the profundus root. It reached the orbit strikingly far back, a fact which perhaps may suggest that the musculus obliquus superior had its origin somewhere from the posterior wall of the orbit, as in *Petromyzon*. Hence we find here quite clearly that the n. trochlearis went almost exactly as in *Petromyzon* (cf. AHLBORN 1883, pl. 13, fig. 2; 1884, pp. 297—299; CORNING 1900, p. 131; JOHNSTON 1902, pl. 1, fig. 1; pl. 8, fig. 30; 1905, pp. 177—178; KRAUSE 1923, fig. 430, p. 803).

As regards the canal V*a* it is not so easy to arrive at any definite opinion of its function as in the case of the canals V*b*, V*c*, V*d*, and IV. As all the usual roots of the trigeminus and profundus nerves seem to have had their exits through the canals V*b*, V*c*, and V*d*, the assumption readily suggests itself, of course, that the canal V*a* may have been traversed by a vessel. But there is also another possibility to be taken into account.

From what will be set forth below, we shall see that the profundus branch of the n. trigeminus in the Cephalaspids was a very well developed independent nerve which supplied the part of the head situated in front of the prespiracular gill-sac. As is generally maintained, therefore, it was certainly the nerve of the premandibular segment. And since, as we shall see, this segment was better developed than in most other forms and in addition must have had visceral musculature, it is very likely that its nerve, the n. profundus, in addition to the components of which it is composed in recent fishes and Cyclostomes just as the other branchial nerves behind it had also a viscero-motor component. That component, if it really existed, probably left the brain as an independent nerve-root and had its exit from the cavum cerebrale cranii through the canal V*a*. The canal V*a* would thus have transmitted the supposed viscero-motor root of the n. profundus.

For the n. abducens there is no independent canal through the cranial wall. It seems not improbable, however, that it entered the canal V*d* through either or both of the two fine canals V_x and V_{xa} and that it thus emerged together with the viscero-motor root of the trigeminus proper. The abducens of fishes may also sometimes accompany the trigeminus through the cranial wall. And at least according to JOHNSTON (1905, pp. 178—179), it would probably in the Petromyzontids regularly be very intimately joined with the roots of the trigeminus proper.

The n. opticus must have entered the orbit through the optic fenestra, probably rather far forward, as there is no canal behind that fenestra through which it could have emerged. We thus see that this fenestra really deserves its name.

From the account given here of the nerve canals of the orbitotemporal region of *C. hoeli* we have, if we summarize it, found the following:

1. The so-called r. profundus trigemini was an independent and more complete nerve than in any other form known. It consisted not only of general cutaneous and communis fibres but in addition probably also of viscero-motor fibres. On account of these facts it will be referred to as the n. profundus, while the remaining part of what is usually called the n. trigeminus will be termed the n. trigeminus proper.
2. The canals V*b* transmitted the general cutaneous root of the n. profundus, while the canal V*a* probably was traversed by the supposed viscero-motor root of the same nerve. The communis fibres for the n. profundus were probably intimately associated with the general cutaneous root.
3. The canals V*c* and V*d* gave passage to the roots of the n. trigeminus proper, V*c* to the general cutaneous root and V*d* to the viscero-motor root. The communis fibres for the n. trigeminus proper probably accompanied the general cutaneous root.
4. The lateralis fibres for the n. profundus and the n. trigeminus proper, as well as the other prootic lateralis fibres, had their exit from the cavum cerebrale cranii together with the roots of the n. facialis and arrived with these roots in the vestibular division of the labyrinth

cavity. Well within this cavity the lateralis fibres for the n. profundus and for the n. trigeminus proper separated immediately from the other prootic lateralis fibres, turned forwards and went through the canal *l* to the orbit.

5. The trigeminus-profundus ganglionic complex was situated with a small portion in the latero-dorsal part of the myodome, but with its chief part it lay just laterally to the myodome in the orbit. The profundus ganglion lay most antero-dorsally of the ganglia. Behind and somewhat ventrally to that followed the ganglion gasseri. The lateralis ganglion was situated ventro-laterally and morphologically posteriorly to the ganglion gasseri just in front of the anterior opening of the canal *l*.
6. The n. abducens had no canal of its own, but, if it was present, it probably accompanied the viscero-motor root of the trigeminus proper to the myodome.
7. The n. trochlearis crossed on its way to the orbit the general cutaneous root of the n. profundus on the dorsal side and was situated on the dorsal surface of that root at the crossing. It reached the orbit strikingly far back.
8. The n. occulomotorius left the cavum cerebrale close behind the optic fenestra straight above the dorsum sellae and far in front of the trigeminus roots.
9. Concerning its nerves the region must have presented very great agreements with the corresponding region in the recent Petromyzontids.

Conditions similar, or at least similar in the main, to those now described in *C. hoeli* with regard to the nerves of the region seem to occur in *Cephalaspis vogti* (pls. 25, 26) and probably in *Hoelaspis* (pl. 45), *Thyestes verrucosus* (pl. 48, fig. 1), *Boreaspis rostrata* (pl. 14) and in the so-called *Thyestes schrenki* (pl. 48, fig. 2).

In the specimen of *Kiaeraspis* from which section series D was made (text-figs. 20—22, 28; section series D, nos. 1—44) we find, on the contrary, certain interesting differences. The canal for the n. oculomotoris (III) lies a little further back than in the forms just treated; and this seems to be a constant feature for it could be exposed in a similar position also in two other specimens (pls. 49, 55). The canal for the pituitary vein (*v. pt*) was, as is well seen, rather wide. The canal for the n. trochlearis left the cavum cerebrale high up, as in *C. hoeli*, but somewhat more forward than in that species and must therefore have crossed the general cutaneous root of the n. profundus already before it entered its canal (IV) through the lateral cranial wall. Both the roots of the n. profundus and the roots of the n. trigeminus proper left the cavum cerebrale through a common wide canal (V) which issues from the latero-ventral part of the cavum cerebrale rather slightly postero-latero-dorsally to the canal for the pituitary vein. In other specimens of the species under consideration, however, the trigeminus canal may very well have been subdivided more or less completely into divisions corresponding to the independent canals of the trigeminus roots in *C.hoeli.* At least in the two specimens figured in plates 49 and 55 there are indications of such a subdivision, the most ventral part of the canal corresponding to the canal V*d* of *C. hoeli* being rather well separated from the other parts.

In *Kiaeraspis* and in certain specimens of *Cephalaspis hoeli* (section series B, nos. 36—38) we find one or a couple of very fine canals (ax_1, ax_2) which issue from the cavum cerebrale in the vicinity of the canal for the n. trochlearis or from the proximal portion of that canal. These canals are known in detail only in the specimen of *Kiaeraspis* used for section series D (nos. 26—43) and, as is seen from text-figs. 20, 22, 27, they seem in that specimen to be rather differently developed on either side of the cavum cerebrale. On the left side there is probably only one canal (ax_2) which goes to the dorsal part of the orbit close behind the canal $v.so_4$; on the right side, on the contrary, there are two canals, one situated anteriorly (ax_1) and one posteriorly (ax_2) to the trochlearis canal. The former of these canals goes antero-dorsally, probably to the superficial parts of the interorbital wall; the latter one could be traced only a short distance upwards. It seems beyond question that these canals were vascular canals; and from the general disposition of the vessels of the region it must be assumed that they transmittet arteries. In this connection, however, attention must, be called to the fact that in several fishes we find an anterior cerebral vein which may leave the cavum cerebrale somewhere in the vicinity of the n. trochlearis (cf. Stensiö, 1925 a, pp. 38—39), but it is, of course, quite excluded that the canals here in question could have transmitted veins from the cavum cerebrale.

The anterior part of the dorsal wall of the cavum cerebrale is always pierced by the wide pineal canal (*pin*, text-figs. 15, 17, 20, 22, 23, 25—27; section series A, nos. 104—110; section series C, nos. 1—17; section series D, nos. 35—42; pl. 13, figs. 1—4; pls. 17, 35, 36, 39, 43, 46; pl. 47, fig. 1). The external opening of this canal (seen in many of the plates) — which, as has been pointed out above (p. 22), varies in shape in different forms — always lies close or immediately anteriorly to the anterior end of the dorsal electric field and not very far behind the posterior division (na_2) of the nasal opening.

The very anterior part of the ventral wall of the region is pierced by a paired rather wide canal (*a. car*, text-figs. 16, 17, 21, 22, 24, 28, 36; section series A, nos. 120—130; section series B, nos. 43—45; section series C, nos. 24—48; pls. 18—20, 22, 23; pl. 23, pls. 28, 29, 44, 45, 51, 52; pl. 54, fig. 1; pl. 55), which from the aortal groove ascends in a postero-dorso-lateral direction to the cavum cerebrale cranii. More exactly this canal opens with its dorsal opening into the antero-lateral part of the fossa hypophyseos somewhat ventro-latero-medially to the anterior angle of the optic fenestra. It is easy to conclude that we are concerned here with the canal for the carotid artery.

In *Cephalaspis hoeli*, as well as in the *Cephalaspis*-species in general and in *Hoelaspis*, a distinct groove goes from the dorsal opening of the carotid canal antero-dorso-laterally on the lateral surface of the cavum cerebrale cranii. This groove then leads into a rather wide canal, *a. fac*, (text-figs. 15—17, 20—25; section series A, nos. 127—135; section series B, nos. 45—50; section series C, nos. 26—35; pls. 21, 28, 29, 45) which passes antero-latero-dorsally within the ethmoidal region. This canal and the groove leading to it obviously transmitted an arterial trunk, a trunk which was a branch from the carotid artery, and which, as we shall see, must have been homologous to the arteria facialis of *Petromyzon*. Hence the canal *a. fac* will be termed here the canal for the arteria facialis.

In *Kiaeraspis* the canal for the arteria facialis goes as an independent canal down to the carotid canal wholly within the lateral cranial wall, and accordingly the facial artery passed there entirely externally to the cavum cerebrale (text-figs. 20—22; 27, 28; section series D, nos. 1—29; pls. 49, 51, 55), while in *C. hoeli* and in *Hoelaspis*, on the contrary, it evidently traversed a short antero-ventro-lateral part of the cavum cerebrale before it reached its canal.

As is obvious from the description given here of the carotid canal, the carotid artery was given off from the cephalic division of the dorsal aorta, which was still unpaired as far forwards as this. Already within the dorsal part of the carotid canal it must evidently have divided into the internal carotid proper, which went to the cavum cerebrale, and an antero-dorso-lateral branch, the facial artery, which entered the canal *a. fac* in the ethmoidal region. While in the *Cephalaspis*-species, and perhaps also in certain other forms, the facial artery traversed a short anterior part of the cranial cavity before it entered its canal in the ethmoidal region, in *Kiaeraspis* it went entirely outside that cavity, within the lateral cranial wall. Very soon after its entrance into the cavum cerebrale the internal carotid proper must have divided into several branches one of which, the ophthalmic artery, went out to the orbit through the membrane which closed the fenestra optica. The groove which from the internal opening of the carotid canal continues postero-laterally towards the antero-ventral part of the optic fenestra may perhaps have lodged the ophtalmic artery.

From the facts just given it is clear that the conditions with regard to the arterial supply of the cavum cerebrale and the ethmoidal region were as in *Petromyzon* (cf. CORI 1906, pp. 34—37, pl. 1; HATTA 1922, pp. 142—150, pl. 22).

Above we have found that the trigeminus ganglionic complex was situated chiefly in the orbit, but that a small part of it also extended postero-dorso-medially into the myodome half of its side. Of the trunks which arose from that ganglionic complex the one representing the truncus-maxillo-mandibularis — or as it will here be called the n. trigeminus proper — certainly immediately after its origin took an antero-lateral course close to the bottom of the orbit. It must have left the orbit through the canal V_2 (text-figs. 4, 13, 23—25, 27, 28, 36; section series A, nos. 112—143; section series B, nos. 41—57; section series C, nos. 81—91; section series D, nos. 1—14; pl. 14; pl. 19, fig. 1; pls. 20, 21; pl. 23, fig. 3; pls. 28, 29, 45, 49, 50, 51, 54, 55, 57, 58), which goes out antero-laterally and ventrally through the part of the visceral endoskeleton situated antero-laterally to the orbit, finally opening into the oralo-branchial chamber; for by its position and course this canal (V_2) is distinctly shown to be serially homologous to the canals VII, IX *a*, etc.; and as in addition there is no other canal from the orbit trough which the trigeminus proper could have emerged, there can be no doubt that it gave passage to that nerve. Below, in the chapter on the visceral endoskeleton we shall have a further opportunity to deal with it, especially with its distal part.

Owing to the considerable size of the canal in *C. hoeli* which transmitted the profundus root, it is clear that the n. profundus must have been a strong trunk. The n. profundus certainly traversed the orbit in the normal way close to the lateral surface of the interorbital wall and dorsally to the n. opticus, which must have entered the orbit very low. In the anterior parts of the orbit it must have turned laterally and somewhat ventrally and have entered the canal V_1 (text-figs. 4, 13, 23—25, 27, 28, 36; section series A, nos. 120—155; section series B, nos. 43—57; section series C, nos. 74—88; section series D, nos. 1—20; pl. 13, fig. 3; pls. 14, 15, 17, 18; pl. 19, fig. 1; pls. 20, 21, 27, 28, 29, 39, 44, 45, 49, 50, 51; pl. 54, fig. 1; pls. 55, 57, 58), which issues from the antero-ventral part of the orbit and pierces the ethmoidal region and the adjacent most anterior parts of the visceral endoskeleton. The canal V_1 opens in the oralo-branchial chamber, as a rule, very far forwards anteriorly to the first interbranchial ridge, but postero-laterally to the area *dpr* (text- figs. 4, 36). From its course and position it is thus easy to understand that the canal V_1 must be serially homologous to the canals V_2, VII, IX *a*, etc.

We shall return to the n. profundus below in the description of the visceral endoskeleton and in the special chapter on the nerves of the cephalic shield. Here I shall merely call attention to the fact that, according to HATSCHEK (1892, p. 152), the n. profundus of *Petromyzon*, has a deep branch which goes down to the mouth.

There is no canal which could have given passage to any nerve corresponding to the r. ophtalmicus superficialis trigemini of fishes, and hence it seems certain that this branch did not exist as an independent branch.

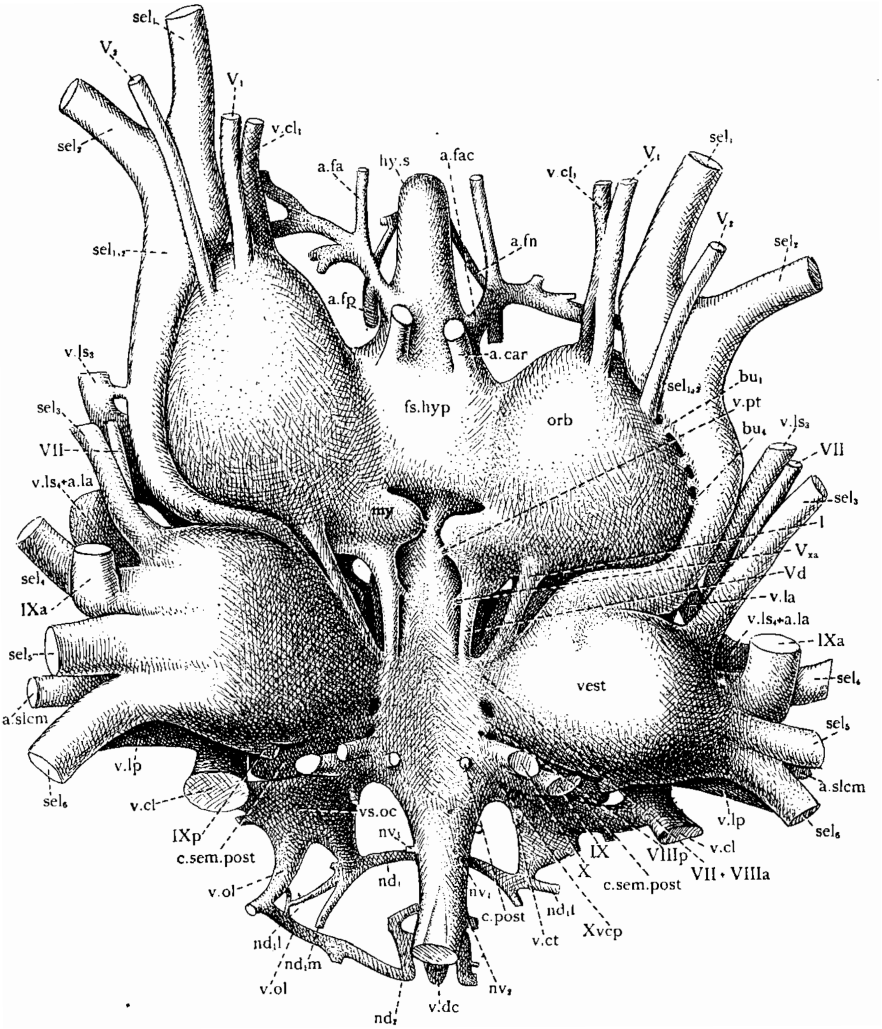
After the account now given of the n. trigeminus proper and the n. profundus we shall turn to the nerves which arose from the lateralis ganglion which, as has been pointed out, must have been situated within the postero-ventro-medial part of the orbit postero-laterally to the ganglion gasseri and which, like that ganglion, formed part of the trigeminus-profundus ganglionic complex. As we know now how the chief anterior portions of the sensory canal system were arranged, and as in addition in recent fishes and Cyclostomes we find that the lateralis nerves always follow more or less exactly the course of the sensory canals innervated by them, it is rater easy to conclude how the lateralis nerves in question in the Cephalaspids must have passed. The chief one of these nerves must evidently, immediately after its origin, have gone antero-laterally in the lateral part of the orbit and have associated more or less soon with the n. trigeminus proper, together with which it left the orbit through the canal V_2. It probably accompanied the n. trigeminus proper throughout the canal V_2, giving of branches to its lateral line portion. Probably already in the posterior part of the orbit, however, it must have given off branches also in a lateral direction through the lateral wall of the orbit, branches which must have traversed at least certain of the posterior ones of the narrow canals denoted in the figures by the letters *bu*, bu_1—bu_5 (text-figs. 24, 28; section series A, nos. 105, 109, 115; section series B, nos. 29, 31—33, 37, 38, 43, 46, 49—52; section series C, nos. 85—90; section series D, nos. 1—3, 14—19; pls. 28, 45, 49, 50). From its course and position it is thus obvious that the lateralis nerve now dealt with must have been homologous with the n. buccalis lateralis of fishes and Cyclostomes (cf. ALLIS 1889, pp. 514—515, pl. 42; 1897, pp. 603—605, pls. 23—26; 1900; 1901, pp. 163—170; 1903 b, pp. 254—258; 1905; 1909 a; 1922 b, pp. 275, 276, pl. 15; 1923 a, p. 211; HERRICK 1899, pp. 332—350; 1900, pp. 279—281; 1901, pp. 199—201; NORRIS & HUGHE 1920, p. 348; HATSCHEK 1892, fig. 11; JOHNSTON 1905; WORTHINGTON, 1905, pp. 170—171, pl. 11; etc.).

A second, though certainly finer, lateralis nerve which also arose from the lateralis ganglion in the orbit must evidently have taken an antero-dorso-medial direction and have associated with the n. profundus, but whether it left this already rather soon and ascended to the roof of the head for the supplying of a lateral sensory groove situated close behind the pineal opening (*pc*, text-figs. 76, 77), or whether it only gave off a dorsal branch for that groove and continued forwards to the ethmoidal region closely associated with the n. profundus it is impossible to decide positively, since it has not been ascertained so far whether any lateral sensory organs were present in front of the nasal opening. In any case it is obvious that it corresponded, at least in part, to the n. ophthalmicus lateralis of fishes and Cyclostomes (cf. ALLIS 1889, pp. 513—514, pl. 42; 1897, pp. 598—603; pl. 30, fig. 38; 1903 b, pp. 249—251; 1909 a; 1922 b, pp. 273—276; 1923 a, pp. 210—211; HERRICK 1899, pp. 351—357; 1900, pp. 274—276; 1901, pp. 201—202; NORRIS & HUGHE 1920, pp. 347—348; JOHNSTON 1905; WORTHINGTON 1905, pp. 170—171; etc.).

The fine canals *bu*, bu_1—bu_5 already referred to probably vary somewhat in number even on both sides in the same specimen but the variations could not be studied in detail. Generally the number of the canals in question seems to be about 3 or 4, but in certain cases it may perhaps be still greater. The majority of the canals are very short, as they lead only to the canal for the two most anterior electric nerves to the lateral electric field, thus the canal lettered $sel_{1,2}$; but one or perhaps two of the most anterior ones may sometimes be longer and instead pass off anteriorly and dorsally to that nerve-canal to the upper surface of the region somewhat antero-laterally to the orbital opening. Since I was unable to find any fine branches issuing dorsally or dorso-laterally from the canal $sel_{1,2}$ this condition would perhaps be thought to be an evidence against the opinion advanced here concerning the course of the branches from the n. buccalis lateralis. But if we realize that these branches, probably soon after their entrance into the canal $sel_{1,2}$, must have broken up into their very fine terminal branches, it is obvious that the openings and canals for these terminal branches when they left the canal $sel_{1,2}$ must have have been extremely delicate — so delicate even that they probably, as a rule, might have been destroyed during the process of fossilisation. It is even possible that these very fine branches, owing to their very minute calibre, were entirely devoid of a lining of perichondral bone, so that on account of this nothing of them could be preserved in the fossils. And accordingly the absence in the fossils of fine canals leading from the canal $sel_{1,2}$ to the dorsal surface of the region close laterally to the orbital entrance does not with necessity imply that such canals did not exist in the Cephalaspids when alive.

Concerning the canals *bu*, bu_1—bu_5 it must be emphasized that they must have given passage not only to lateralis nerves but also to the general cutaneous branches from the n. trigeminus proper and in addition they may perhaps have given passage also to small arteries and to veins which went to the orbit.

Whether in the Cephalaspids there was, as in *Petromyzon* (JOHNSTON 1905, pl. 5), an anastomosis between the lateralis part of the



Text-fig. 24 A. *Cephalaspis hoeli* Cast of the cranial cavity, the labyrinth cavity, the orbits and the canals related to these cavities in ventral view. The figure has been drawn after a model in wax made after section series A. 10/1.

(Text-fig. 24 A continued.)

a. car, canal for the carotid artery; *a. fa*, anterior branch of the canal for the facial artery; *a. fac*, canal for the facial artery; *a. fn*, canal for a branch of the facial artery to the hypophysial sac; *a. fp*, canal for a dorso-posterior branch of the facial artery; *a. slcm*, canal for a dorso-lateral superficial arterial trunk arisen by the union of the two most posterior dorso-lateral superficial arteries; bu_1—bu_4 canals for branches from the n. buccalis lateralis, for general cutaneous branches and perhaps also for arteries and veins; *c. post*, canal for the posterior encephalic artery; *c. sem. post*, division of the labyrinth cavity for the canalis semicircularis posterior; *fs. hyp*, fossa hypophyseos; *hy. s*, division of the ethmoidal cavity for the hypophyseal sac; *l*, canal for the lateralis fibres to the trigeminus-profundus ganglionic complex; *my*, myodome; nd_1, canal for the myelonal vein 1 and probably also for the dorsal root of the spino-occipital nerve 1; $nd_1.l$, canal probably for a vein; nd_2, canal for the myelonal vein 2 and probably also for the dorsal root of spino-occipital nerve 2; $nd_1 m$, postero-medial branch of the canal nd_1 a branch which probably transmitted the dorsal root of the first spino-occipital nerve; nv_1, canal for the ventral root of or for the entire spino occipital nerve 1. In addition this canal transmittet the myelonal artery 1; nv_2, canal for the ventral root of the spino-occipital nerve 2, or for the entire spino-occipital nerve 2. In addition it transmitted the myelonal artery 2; *orb*, orbit; $sel_{1,2}$, common canal for the two most anterior nerves to the lateral electric field; sel_3—sel_6, canals for the nerves 3—6 to the lateral electric field; *v. cl*, canal for the vena capitis lateralis; $v.\,cl_1$, canal for the preorbital portion of the vena capitis lateralis; *v. ct*, canal for a vein opening into the v. cerebralis posterior at the transition to the occipital vein sinus; *vest*, vestibular division of the labyrinth cavity; *v. la*, *v. lp*, canals for lateral tributaries to the vena capitis lateralis; $v.\,ls_3$, canal for the dorso-lateral superficial vein 3; $v.\,ls_4 + a.\,la$, common canal for the dorso-lateral superficial vein 4 and the anterior dorso lateral-superficial arterial trunk arisen by the union of the anterior dorso-lateral superficial arteries; *v. ol.* canal for the lateral occipital vein; *v. pt*, canal probably for the pituitary vein; *vs. oc*, occipital vein sinus; V*d*, canal probably for the viscero motor root of then trigeminus proper; V_{xa}, canal perhaps for a part of the n. abducens; V_1, canal for the n. profundus; V_2, canal for the n. trimiginus proper; VII, canal for the n. facialis; VII + VIII *a*, acustico-facialis canal. This canal transmitted the roots of the n. facialis, all the prootic lateralis fibres, the electric nerve fibres to the electric fields and at least the anterior branch of the n. acusticus; VIII *p* canal for the posterior branch of the n. acusticus; IX, the glossopharyngeus branch of the vagus canal; IX *a*, canal for the n. glossopharyngeus after this nerve had traversed the labyrinth cavity; IX *p*, canal for the n. glossopharyngeus to the labyrinth cavity; X, branch of the vagus canal for vagus roots; X*vcp* branch of the vagus canal for the vena cerebralis posterior.

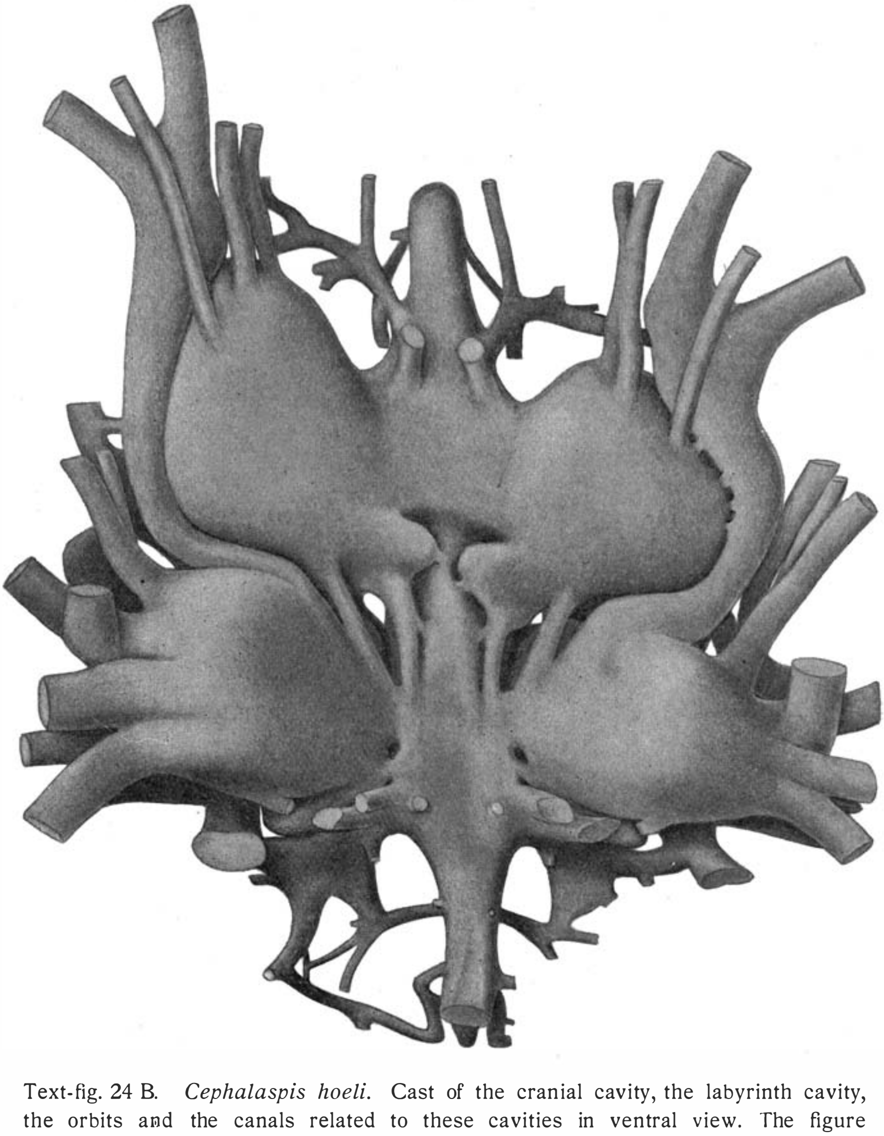
trigeminus ganglionic complex and the lateralis part of the vagus ganglionic complex cannot be ascertained. If such an anastomosis was present it must have been situated, together with the vena capitis lateralis, in the canal *v. cl*, for besides this there is no canal which could have lodged it. It deserves to be added that it may very well be thought to have had such a position.

The canal $sel_{1,2}$, which has already been dealt with to some extent, enters the region from the antero-lateral part of the otic region, passing forwards close laterally (ventrally) to the orbit (text-figs. 23—25, 27—28; section series A, nos. 86—155; section series B, nos. 24—57; section series C, nos. 68—94; section series D, nos. 1—20; pls. 14, 15, 17, 18, 21, 28, 29, 45, 49, 50, 54, 55). In the *Cephalaspis*-species it divides into its two branches sel_1 and sel_2 just antero-laterally to the orbit. On the contrary in *Hoelaspis*, *Boreaspis* and *Kiaeraspis*, as has already been pointed out, it remains as a single wide canal still farther antero-laterally — in *Kiaeraspis* even as far as its very entrance into the lateral electric field.

In the anterior and lateral parts of the region we find, as will be described in detail below in the account of the ethmoidal region, several branches of the canal for the arteria facialis. The disposition of these branches is well seen in text-figs. 44, 46, 47, 49, 51 and in pls. 27, 28, 29, 30, and 39. At least in *Cephalaspis hoeli* the postero-dorsal parts of the interorbital wall received their arterial blood through an anterior branch (*a.* dsm_1, text-figs. 23, 25; section series A, nos. 78—91; section series B, nos. 34—39) of the postorbital superficial artery, which issued from the cavum cerebrale in the roof of the otic region through the canal *a. dsm.*

The superficial parts of the ethmoidal region and the adjacent parts of the visceral endoskeleton in front of that region were, as we shall see, drained by a large vein which entered the orbit at the anterior end through the canal *v.* cl_1, slightly dorso-medially to the canal for the n. profundus. As we shall find, this vein corresponded exactly to the anterior portion of the v. capitis lateralis of *Petromyzon* (cf. Cori 1906, pp. 48—52; Hatta 1922, pp. 180—185), and the term v. capitis lateralis will therefore be employed for it in the subsequent account. Well within the orbit it went dorsally to the n. profundus, which it probably accompanied more or less closely as far backwards as to the profundus ganglion. Beyond that ganglion it probably turned more laterally and upwards along the posterior wall of the orbit and during this part of its course it probably received the presumed pituitary vein. Finally it left the orbit through the canal *v. cl.*

In the specimen of *Kiaeraspis* used for section series D (text-fig. 27; section series D, nos. 35—50) there are severals canals *v.* so_1— *v.* so_4, which from the dorsal parts of the infraorbital wall go down-



Text-fig. 24 B. *Cephalaspis hoeli.* Cast of the cranial cavity, the labyrinth cavity, the orbits and the canals related to these cavities in ventral view. The figure has been drawn after the same model in wax as text-figs. 23 and 24 A.

wards to the orbit. These canals, most of which branch abundantly in their distal parts, open into the dorsal and antero-dorsal parts of the orbit and are four in number on the left side and five on the right side. As far as can be judged, these canals transmitted veins which drained the parts of the interorbital wall that received their arterial blood by posterior branches from the arteria facialis (cf. p. 112 above and the chapter on the ethmoidal region below), by branches from the postorbital superficial artery (cf. p. 73 above), and by the small supposed arteries, which traversed the canals ax_1 and ax_2. The veins lodged in the canals $v. so_1$—$v. so_4$ certainly, after their entrance into the orbit, emptied into the vena capitis lateralis. 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 trasversal lateral line groove (*pc*, text-figs. 76, 77) situated close behind the pineal opening.

The superficial part of the region laterally to the posterior part of the orbit was drained by tributaries to the dorso-lateral superficial vein 3, which was lodged in the canal $v. ls_3$ (text-figs. 23—25; 27, 28, section series A, nos. 89—113; section series C, nos. 80—107; section series D, nos. 2—8; pls. 20, 21, 25, 27—31, 39, 45, 49, 50, 55). While, as has been pointed out, this canal, $v. ls_3$, in the *Cephalaspis*-species goes to the postero-latero-ventral part of the orbit, in *Kiaeraspis* and *Hoelaspis* it goes instead to the most anterior part of the canal *v. cl.* Accordingly in the *Cephalaspis*-species the dorso-lateral superficial vein 3 emptied into the v. capitis lateralis within the very posterior part of the orbit, whereas, on the contrary, in *Kiaeraspis* it did not join the same vein until close posteriorly to the orbit in the most anterior part of the otic region. Since, as has been called attention to already in the description of the otic region, in many cases not only the dorso-lateral superficial vein 4, but sometimes also the dorso-lateral superficial vein 5 had joined the dorso-lateral superficial vein 3, the proximal part of this was a rather wide trunk. In such cases when one or both of the dorso-lateral superficial veins 4 and 5 had joined 3 the canal which transmitted the proximal part of this has in the figures and plates generally been denoted by the letters *v. la.*

Finally it may be mentioned here that in the specimen of *Kiaeraspis* from which section series D was made a very fine canal went out from the right orbit into the ethmoidal region somewhat dorso-medially to the canal $v. cl_1$. As this fine canal (*ex*, text-fig. 27; section series D, nos. 15—21) probably is not constantly present in the Cephalaspids it seems most probable that it transmitted a vessel, conceivably a vein. We shall return to that canal below in the description of the ethmoidal region.

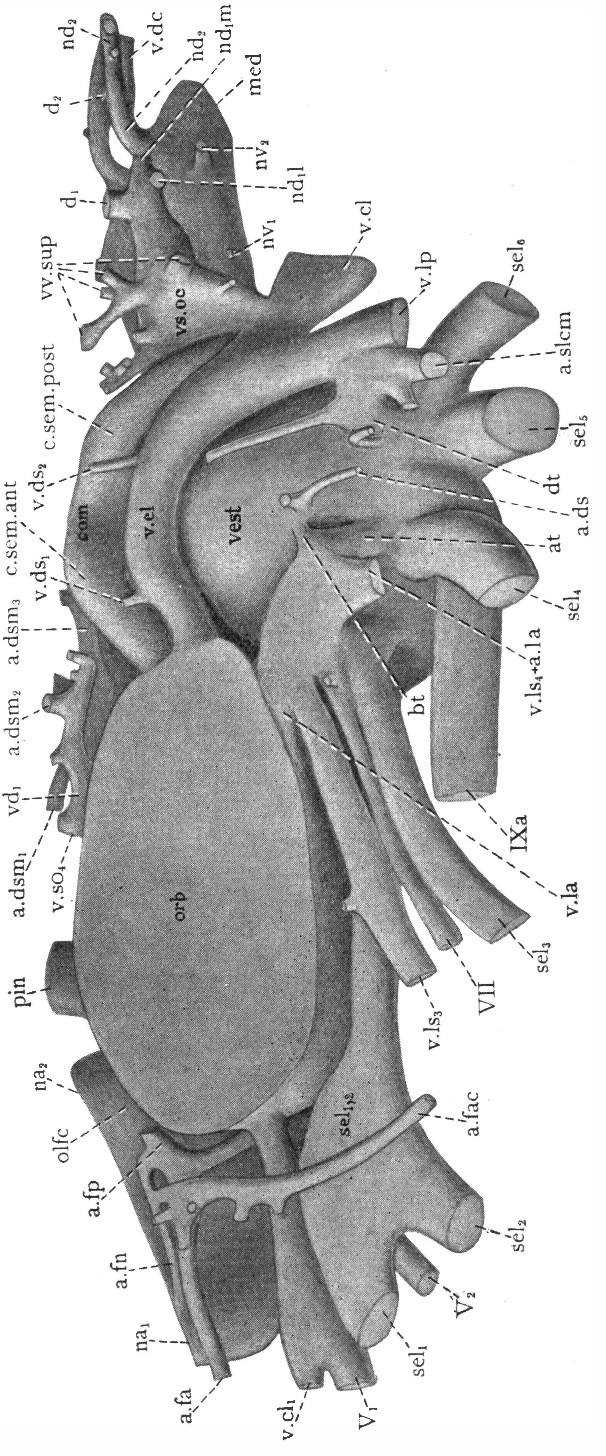
Ethmoidal region. — Since, as we shall see, the rostral parts of the shield (cf. the chapter on the *Heterostraci* below), probably as far back as to the nasal opening, have been formed by the exessively developed upper lip and thus are of a visceral origin, the anterior boundary of the ethmoidal region may be considered to be at the anterior end of the nasal aperture. The ethmoidal region (text-figs. 4, 7, 8, 13) is thus continuous with and passes over into the visceral endoskeleton not only laterally but also rostrally. Its lateral boundary may for practical reasons be considered to be along a longitudinal line passing forwards parallel with the longitudinal axis of the cephalic shield from a point somewhat laterally to the antero-ventral corner of the orbit. Finally posteriorly it reaches with its lateral part of each side to the orbit, forming the anterior boundary of this, while, on the contrary, with its median part it extends somewhat further backwards between the orbits, so that in fact it forms at least the most antero-dorsal part of the interorbital wall.

With regard to dimensions the ethmoidal region, as thus defined, is always short and broad, its length constituting only about one third of the breadth. While, as a whole, it decreases in height forwards it is, however, throughout its length considerably higher in its median than in its lateral parts.

In accordance with the general configuration of the cephalic shield, the region occupies such a position that it slopes more or less forwards and in addition it is always somewhat arched in transversal direction with the convexity upwards and the concavity downwards. It presents a dorsal and a ventral surface and in addition a paired posterior surface.

The dorsal surface (section series A, nos. 118—155; section series B, nos. 51—57; section series C, nos. 1—95; section series D, nos. 1—35; pl. 39) which is continuous posteriorly with the dorsal surface of the orbitotemporal region and laterally with the upper (outer) surface of the visceral endoskeleton faces more or less antero-dorsally. On its most posterior part we find the unpaired external nasal opening, which, as we have seen (p. 22 above), consists of an anterior and a posterior division which are more or less circular or oval, and which are connected with each other by a third narrow, slit-like division (text-figs. 3, 7, 8, 23, 27). Around the nasal opening there must have been an impression of the circumnasal fossa since this fossa had pressed the dermal bone beneath it rather much downwards into the endoskeleton..

The ventral surface (text-figs. 2 A, 4, 13, 36; section series A, nos. 129—155; section series B, nos. 51—57; section series C, nos. 1—95; section series D, nos. 1—12; pls. 14, 15, 21, 22; pls. 44, 51, 52; pl. 54, fig. 1; pl. 56, fig. 1; pl. 57; pl. 62, fig. 1), which is continuous posteriorly with the ventral surface of the orbitotemporal region and laterally and anteriorly with the ventral (inner) surface of the visceral endoskeleton, forms part of



Text-fig. 25. *Cephalaspis hœli* n. sp.

Text-fig. 25. *Cephalaspis hoeli.* Cast of the cranial cavity, the labyrinth cavity, the orbit and the canals related to these cavities in lateral view. The figure drawn after a model in wax made after section series A. Magnification about $^{16}/_{1}$.

a. ds, canal for a fine artery for the dorso-lateral part of the otic region: *a. dsm*$_1$, *a. dsm*$_2$, *a. dsm*$_3$, canals for branches of the postorbital superficial artery; *a. fa*, anterior branch of the canal for the facial artery; *a. fac*, canal for the facial artery; *a. fn*, canal for a branch of the facial artery to the external opening of the hypophysial sac; *a. fp*, canal for a dorso-posterior branch of the facial artery; *a. slcm*, canal for a posterior dorso-lateral superficial arterial trunk; *at*, *bt*, canals for the n. facialis and for the anterior dorso-lateral superficial arterial trunks; *com*, commissural division of the labyrinth cavity; *c. sem. ant*, division of the labyrinth cavity for the canalis semicircularis anterior; *c. sem. post*, division of the labyrinth cavity for the canalis semicircularis posterior; d_1, canal for a vein from the dorsal electric field and in addition probably for the most dorsal part of the ductus endolymphaticus; d_2, canal for a vein from the dorsal electric field; *dt*, canal for an arterial branch; *med*, division of the cranial cavity for the medulla oblongata; *na*$_1$, opening of the hypophysial sac; *na*$_2$, nasal opening proper; *nd*$_1$, canal for the myelonal vein 1 and probably also for the dorsal root of the spino-occipital nerve 1; *nd*$_1$ *l*, canal probably for a vein; *nd*$_1$ *m*, postero-medial branch of the canal *nd*$_1$, a branch which probably transmitted the dorsal root of the first spino-occipital nerve; *nd*$_2$, canal for the myelonal vein 2 and probably also for the spino-occipital nerve 2; *nv*$_1$, canal for the ventral root of or for the entire spino-occipital nerve 1 and in addition also for the myelonal artery 1; *nv*$_2$, canal for the ventral root of the spino-occipital nerve 2, or for the entire spino-occipital nerve 2. The canal gave also passage to the myelonal artery 2; *olfc*, part of the ethmoidal cavity, that lodged the olfactory organ; *orb*, orbit; *pin*, pineal canal; *sel*$_{1,2}$, common canal for the first and second nerves to the lateral electric field; *sel*$_1$—*sel*$_6$, canals for the electric nerves to the lateral electric field; *v. cl*, canal for the vena capitis lateralis; *v. cl*$_1$, canal for the preorbital portion of the vena capitis lateralis; *vd*$_1$, vein canal leading to the orbit; *v. dc*, cavity for a vein sinus; *v. ds*$_1$, *v. ds*$_2$, canals for veins from the dorsal part of the otic region; *vest*, vestibular division of the labyrinth cavity; *v. la*, *v. lp*, canals for lateral tributaries to the vena capitis lateralis, lateral tributaries formed by the confluence of the posterior four dorso-lateral superficial veins; *v. ls*$_3$, *v. ls*$_4$, canals for the dorso-lateral superficial veins 3 and 4; *v. ls*$_4$ + *a. la*, common canal for the dorso-lateral superficial vein 4 and the anterior dorso-lateral-superficial arterial trunk arisen by the union of the anterior dorso-lateral superficial arteries; *vs. oc*, occipital vein sinus; *v. so*$_4$, canal for a vein from the dorsal side of the interorbital wall and the anterior parts of the dorsal electric field; *vv. sup*, canals for superficial veins leading to the occipital vein sinus; V_1, canal for the n. profundus; V_2, canal for the n. trigeminus proper; VII, canal for the n. facialis from the labyrinth cavity; *IXa*, canal which transmitted the n. glossopharyngeus from the labyrinth cavity.

the upper surface of the oralo-branchial chamber and is lined throughout by the external perichondral bone-layer. Its median part is occupied by an anterior portion of the aortal ridge (*r. aort*) with its groove — the aortal groove — and on each side of that portion of the aortal ridge there is the often rather deep subnasal fossa (*f. sn*). In addition we find, in certain forms such as *Kiaeraspis* and *Hoelaspis*, regularly on the surface in question the most dorsal part of the interbranchial ridge 2 (*ibr*$_2$, text-figs. 4, 13, 36; pl. 44; pl. 46, fig. 1; pls. 51, 52); and it is particularly worthy of notice that the interbranchial ridge 2 of the said forms extends to the aortal ridge and is grooved in its longitudinal direction in the vicinity of that ridge. As the groove leads to the aortal groove, it is not difficult to conclude that it must have been caused by an efferent branchial artery — in fact, as we shall find, the second one counted from in front.

The posterior surface, which, as has been pointed out, is paired, forms the anterior surface of the orbit of its side and is somewhat concave both in dorsi-ventral and latero-medial directions.

Within the median high part of the region that is situated above the aortal ridge there is a cavity which forms the direct anterior continuation of the cavum cerebrale cranii and which, like that, is lined by the inner perichondral bone-layer. Since this cavity leads to and opens anteriorly by means of the nasal opening it is at once quite clear that at least partly it must have lodged the olfactory organ and that therefore, at least within the chief part, it cannot have been occupied by the brain. For the sake of brevity it will be referred to in the sequel as the ethmoidal cavity.

The ethmoidal cavity, as thus defined (text-figs. 15—17, 20—25; 27, 28; section series A, nos. 118—155; section series B, nos. 51—57; section series C, nos. 1—45; section series D, nos. 1—35; pl. 13, figs. 2, 3; pl. 14; pl. 19, fig. 1; pls. 21, 28, 45, 49; pl. 54, fig. 1; pls. 55—58), reaches forwards exactly as far as the nasal opening; backwards, on the contrary, it reaches somewhat further than that. Most posteriorly it is high — even as high as the cranial cavity — but decreases rapidly in height forwards so that at the anterior end it is usually rather low. As a whole, it is narrow, but it widens, however, somewhat posteriorly at the transition into the cranial cavity.

Corresponding to the three divisions of the nasal aperture there may be distinguished in the ethmoidal cavity three divisions — an antero-ventral one, a middle one, and a postero-dorsal one.

The first mentioned of these divisions, which is the longest one of the three, stretches from the anterior oval or circular anterior division (na_1) of the nasal aperture downwards and posteriorly to the hypophyseal fossa, thus constituting the anterior and ventral part of the ethmoidal cavity (*hy. s*, text-figs. 15—17, 20—25, 27, 28). Until rather close anteriorly to the fossa hypophyseos it retains approximately the diameter of the anterior division of the nasal aperture and as, on account of that, it is considerably thicker than the middle division, it appears as a tube which leads from the anterior division of the nasal aperture to the fossa hypophyseos, a tube which, however, is not closed towards the middle division (pl. 19, fig. 1; pls. 20—23, 45, 49, 55—58).

The middle division (text-figs. 15, 17, 20, 22, 23—25, 27, 28) lies next dorsally to the antero-ventral division and beneath the middle slit-like division of the nasal opening. Ordinarily it is much narrower than the other two divisions, but becomes, however, somewhat wider towards these and posteriorly.

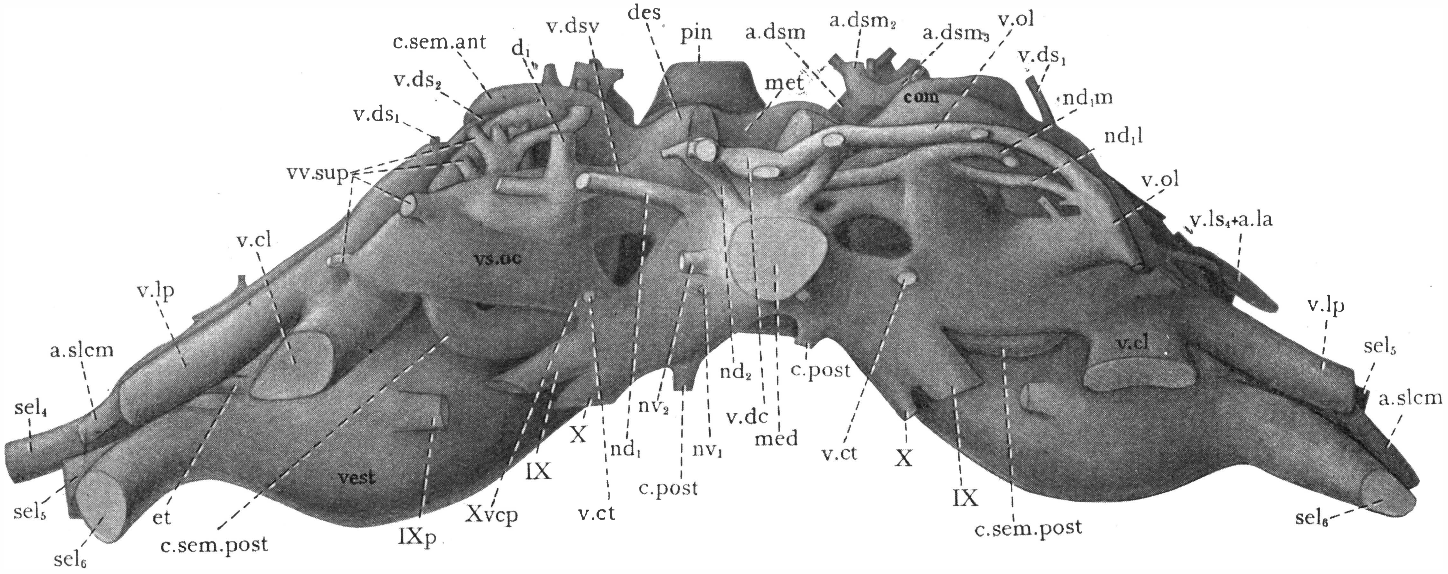
Finally the postero-dorsal division (*olfc*, text-figs. 15, 17, 20, 22, 23—25, 27, 28; pl. 13, fig. 3; pl. 47, fig. 1) goes from the postero-dorsal circular or oval division of the nasal aperture (na_2) postero-ventrally or ventrally to the most antero-dorsal part of the orbitotemporal division of the cranial cavity and, like the antero-ventral one, is tube-shaped. It is open on the ventral side towards the middle division.

As we shall see from the description of the cranial cavity below, the telencephalon was situated in the antero-dorsal part of the orbitotemporal division of the cranial cavity and thus definitely behind the ethmoidal cavity. Since now the postero-dorsal division of the ethmoidal cavity leads to that very part of the cranial cavity it must obviously have lodged the chief dorsal part of the olfactory organ, while a ventral part of that organ probably occupied the middle division of the same cavity (text-fig. 32). The antero-ventral division of the ethmoidal cavity, on the contrary, cannot have had anything to do with the olfactory organ, but must have lodged an hypophyseal (pituitary) sac homologous to that of recent Cyclostomes. Since the floor of the fossa hypophyseos is not perforated by any canal, except by the carotid canal, it is fully obvious that the hypophyseal sac here (text-fig. 32) must have ended blindly in the fossa hypophyseos and hence it was shorter even than in the adult *Petromyzon* (PARKER & HASWELL 1910, fig. 798; GOODRICH 1909, fig. 34. KRAUSE 1923, fig. 418). We thus find that the postero-dorsal and middle divisions of the ethmoidal cavity may alone be considered to have constituted the nasal cavity proper; and as a consequence of this the opening which has been called above the nasal aperture was in fact a naso-pituitary aperture, quite like that in the recent Cyclostomes (cf. BRIDGE 1904, pp. 390—393).

In the Cephalaspids, when they were alive, the cavum cerebrale and the ethmoidal cavity were certainly separated from each other by a membrane of thick dural connective tissue. This membrane was, of course, pierced in its dorsal parts by the olfactory nerves, which went to the postero-dorsal division of the ethmoidal cavity (cf. text-fig. 32).

As is well shown by the section figures (section series A, nos. 129—155; section series B, nos. 51—57; section series C, nos. 1—45) the ventral wall and the ventral parts of the lateral walls of the ethmoidal cavity are always rather thin; and, as is also evident from the section figures, it is the ethmoidal cavity which by its height causes the aortal ridge on the posterior part of the region to be situated almost in the same level as in the anterior part of the orbitotemporal region.

As we have already found, the n. profundus left the orbitotemporal region at the antero-ventral part of the orbit, and consequently so far laterally that it perforated the lateral, thin part of the ethmoidal region.



Text-fig. 26. *Cephalaspis hoeli.*

Text-fig. 26. *Cephalaspis hoeli.* Cast of the cranial cavity, the labyrinth cavities and the canals related to these cavities. Posterior view. After a model in wax made after section series A. Magnification $^{20}/_{1}$.

a. dsm, $a.\,dsm_2$, $a.\,dsm_3$, canal for the postorbital superficial artery and for two of its branches; *a. slcm*, canal for a dorso-lateral-superficial arterial trunk arisen by the union of the two most posterior dorso-lateral superficial arteries; *com*, commissural division of the labyrinth cavity; *c. post*, canal for the posterior encephalic artery; *c. sem. ant*, division of the labyrinth cavity for the canalis semicircularis anterior; *c. sem. post*, division of the labyrinth cavity for the canalis semicircularis posterior; d_1, short canal for a vein from the dorsal electric field, and in addition probably for the dorsal part of the ductus endolymphaticus; *des*, canal for the nerve to the dorsal electric field; *dx*, canal for a nerve or for an artery or for both; *et*, canal for an artery; *med*, division of the cavum cerebrale cranii for the medulla oblongata; *met*, division of the cavum cerebrale cranii for the metencephalon; nd_1, canal for the myelonal vein 1 and probably also for the dorsal root of the spino-occipital nerve 1; $nd_1\,l$, canal probably for a vein; $nd_1\,m$, postero-medial branch of the canal nd_1, a branch which probably transmitted the dorsal root of the first spino-occipital nerve; nd_2, canal for the myelonal vein 2 and probably also for the spino-occipital nerve 2; nv_1, canal for the ventral root of or for the entire spino-occipital nerve 1 and in addition for the myelonal artery 1; nv_2, canal probably for the ventral root of the spino-occipital nerve 2 and in addition also for the myelonal artery 2; *pin*, pineal canal; sel_4—sel_6, canals for the three posterior nerves to the lateral electric field; *v. cl*, canal for the vena capitis lateralis; *v. ct*, canal probably for a vein opening into the v. cerebralis posterior at the transition to the occipital vein sinus; *v. dc*, cavity for a vein sinus; $v.\,ds_1$, $v.\,ds_2$, canals for veins from the dorsal parts of the otic region; *v. dsv*, canal for the otical vein and in addition probably for the ductus endolymphaticus; *vest*, vestibular division of the labyrinth cavity; *v. lp*, canal for a lateral tributary to the vena capitis lateralis; $v.\,ls_4 + a.\,la$, common canal for the dorso-lateral superficial vein 4 and the anterior dorso-lateral-superficial arterial trunk arisen by the union of the anterior dorso lateral superficial arteries; *v. ol*, canal for the lateral occipital vein; *vs. oc*, occipital vein sinus; *vv. sup*, canals for superficial veins leading to the occipital vein sinus; IX, division of the vagus canal for the n. glossopharyngeus; IX *p*, canal for the passage of the n. glossopharyngeus to the labyrinth cavity; X, branch of the vagus canal for the vagus roots: X *vcp*, branch of the vagus canal for the vena cerebralis posterior.

Its canal V_1 through this region, which is well displayed in several specimens (text-figs. 23—25, 27, 28; section series, A, nos. 122—155; section series B, nos. 43—57; section series C, nos. 72—88; section series D, nos. 1—20; pl. 13, fig. 3; pls. 14, 15, 17, 18; pl. 19, fig. 1; pls. 20, 21, 27, 28, 29, 45, 48, 49, 50, 54—58), is always rather wide and goes anteriorly and somewhat laterally to the rostral part of the visceral endoskeleton, opening far forwards into the oralo-branchial chamber. In the specimen of *Hoelaspis* shown in pl. 45 a short branch was given off from this canal somewhat anteriorly to the orbit, a branch (V_{1v}) which went ventro-medially and opened into the oralo-branchial chamber not far laterally to the deapest part of the subnasal fossa (*f. sn.*). As we shall see in the chapter on the visceral endoskeleton below, this branch has such a position that it seems to have transmitted a visceral ramus from the n. profundus; and thus in this respect the n. profundus would have been developed quite as those branchial nerves behind it which also had a visceral ramus.

A short postero lateral part of the region may in many cases (pls. 17, 18, 28, 45, etc.) be traversed by the canal $sel_{1,2}$ (*Kiaeraspis, Hoelaspis*) or, when this canal branches already close to the orbit, by its first branch — the canal sel_1 (*Cephalaspis*). Not rarely we find also in the postero-lateral part of the region the most anterior one or the most anterior ones of the canals bu_1—bu_5, already dealt with above.

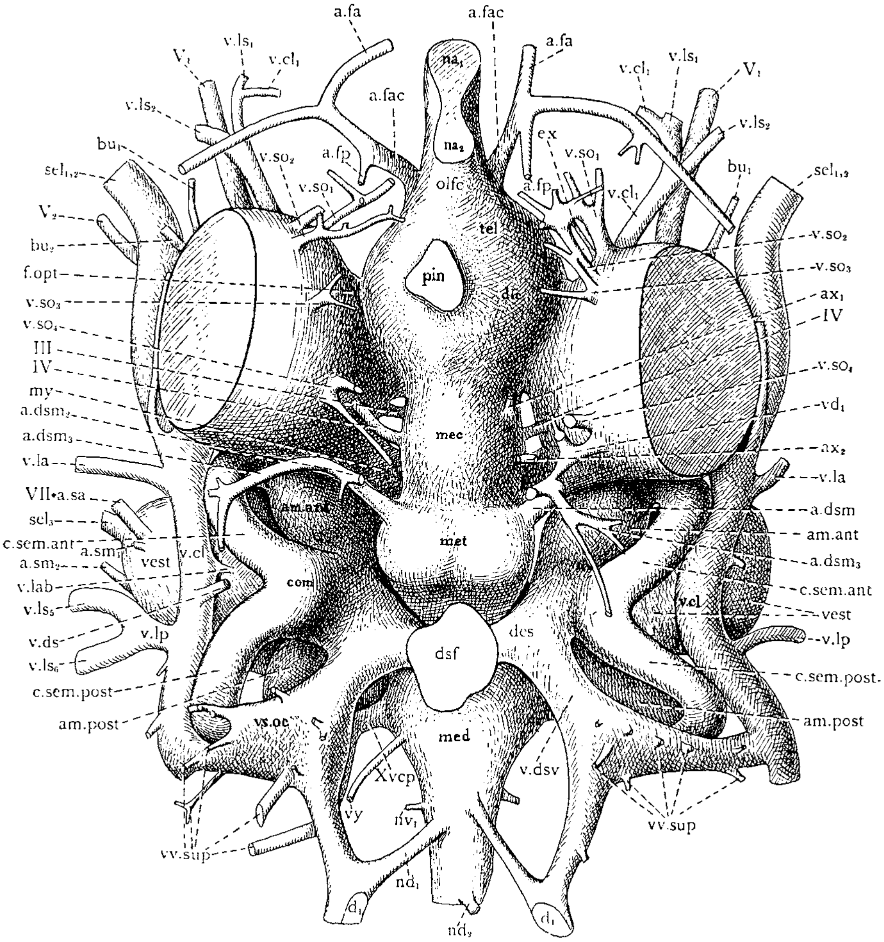
The canal for the arteria facialis (*a. fac*), as has been set forth above (p. 112), has its origin either from the dorsal part of the carotid canal (*Kiaeraspis*, text-figs. 21, 22, 28; section series D, nos. 1—29; pls. 49, 55) before this opens into the cranial cavity or from the most antero-ventral part of the cranial cavity somewhat antero-dorsally to the opening of the carotid canal into that cavity (*Cephalaspis*, text-figs. 16, 17, 24; section series A, nos. 127—155; section series B, nos. 45—57; section series C, nos. 27—82; pl. 19, fig. 1; pls. 21, 28, 29; *Hoelaspis*, pl. 45). In the latter case, however, it is continued downwards to the internal opening of the carotid canal by a groove on the lateral surface of the cranial cavity. From its origin it goes first dorsally and slightly antero-laterally within the part of the ethmoidal region lying between the ethmoidal cavity and the orbit (text-figs. 23—25, 27, 28, 44, 46, 47, 49, 51; section series A, nos. 127—155; section series B, nos. 45—57; section series C, nos. 27—82; section series D, nos. 1—29; pls. 21, 27, 28, 45, 49, 55). Most ventrally it is there situated close to the ethmoidal cavity, gradually withdrawing from that cavity upwards. During its course upwards several fine branches issue from it to the ethmoidal cavity and, in certain cases, also to the anterior end of the orbitotemporal division of the cranial cavity. Having arrived somewhat beneath the dorsal surface of the region, it suddenly curves laterally and at or close to this point it gives off two rather wide branches, one forwards, the other backwards.

The former of these branches (*a. fa*, text-figs. 23, 24, 25, 27, 28, 44, 46, 47, 49; section series A, nos. 136—155; section series B, nos. 54—57; section series D, nos. 13—23; pls, 27, 28; pl. 40, fig. 5; pls. 45, 49, 55) goes forwards somewhat laterally to the nasal aperture, soon reaching the dorsal surface of the region and commencing to branch frequently. It could be distinctly traced until somewhat in front of the anterior division of the nasal aperture, then breaking up into very numerous and fine twigs which form part of the subaponeurotic vascular plexus on the rostral part of the visceral endoskeleton. The posterior branch (*a. fp*, text-figs. 23, 24, 25, 27, 28, 44, 46, 49; section series A, nos. 127—135; section series B, nos. 51—54; section series D, nos. 20—26; pl. 39; pl. 40, fig. 5) immediately takes a postero-dorsal course and goes to the fossa circumnasalis and the upper surface of the prepineal part of the interorbital wall. Its mode of branching in the fossa circumnasalis is well displayd by the specimen figured in pl. 39.

At least in several cases one or a few additional branches are sent off from the canal for the arteria facialis at the point where its canal turns laterally (pl. 27). In the specimen of *Cephalaspis hoeli* from which section series A was made one of these additional branches which is paired (*a. fn*, text-figs. 15—17, 23, 24, 25; section series A, nos. 132—146) goes to the upper part of the division of the ethmoidal cavity that lodged the hypophyseal sac, opening into that rather far back close to the transition to the middle division of the same cavity. It is quite conceivable that the arterial branch transmitted by it carried blood not only to the hypophyseal sac but also to the adjacent anterior part of the olfactory organ.

Distally to the branches described, the canal for the arteria facialis — which there, as has already been mentioned, has a lateral course — soon ascends to the dorsal surface of the region, on which it continues laterally or in several cases laterally and somewhat posteriorly, giving off branches especially forwards (text-figs. 44, 46, 47; pls. 29, 30, 39; pl. 40, fig. 5; pl. 55) — branches which all pass over into the subaponeurotic vascular plexus. In certain forms it comes during this part of its course rather close to the orbital entrance (*Kiaeraspis*, pl. 55; *Cephalaspis heintzi*, pl. 30). Somewhat antero-laterally to the orbital entrance it generally breaks up into three main branches all of which also break up into fine rami which form part of the subaponeurotic vascular plexus. One of these three main branches (*a. iom*, text-figs. 44, 46, 47, 49, 51; pls. 25, 27, 30, 39; pl. 40, fig. 5; pls. 49, 50, 55), immediately after its origin, turns posteriorly to the orbitotemporal region, continuing backwards on that region on the dorsal side of the canal $sel_{1,2}$ and thus close laterally (ventrally) to the orbital entrance, and sending out one or two rather wide branches on the lateral side to the dorsal (external) surface of the adjacent part of the visceral endoskeleton. It seems not to have reached backwards beyond the orbital entrance, and, as is shown by the figures cited its lateral branches are situated on the part of the visceral endoskeleton that falls between the canals for the n. trigeminus proper and the n. facialis. In virtue of its position in relation to the orbit, this branch is called here the medial infraorbital branch.

The branch (*a. iol*, text-figs. 44, 46, 47, 49, 51; pls. 27, 29, 30, 39, 55) following next anteriorly to the medial infraorbital branch has its origin from the canal for the arteria facialis either together with the former branch or together with the most anterior one. It seems generally to be the widest one of the three and goes postero-laterally to the antero-ventral portion of the part of the visceral endoskeleton situated between the canals for the n. trigeminus proper and the n. facialis; but it also sends branches to the lateral electric field. We shall refer to it in the subsequent account as the lateral infraorbital branch.



Text-fig. 27 A. *Kiaeraspis auchenaspidoides.* Cast of the cranial cavity, the labyrinth cavities the orbits and the canals related to these cavities from the dorsal side. After a model in wax made after section series D. Magnification $^{18}/_{1}$.

a. dsm, canal for the postorbital superficial artery; *a. dsm*$_1$, *a. dsm*$_2$, *a. dsm*$_3$, branches from the canal *a. dsm*; *a. fa*, anterior branch of the canal for the facial artery; *a. fac*, canal for the facial artery; *a. fp*, canal for a dorso-posterior branch of the facial artery; *am. ant*, swelling for the ampulla anterior; *am. post*, swelling for the ampulla posterior

(Text-fig. 27 A continued.)

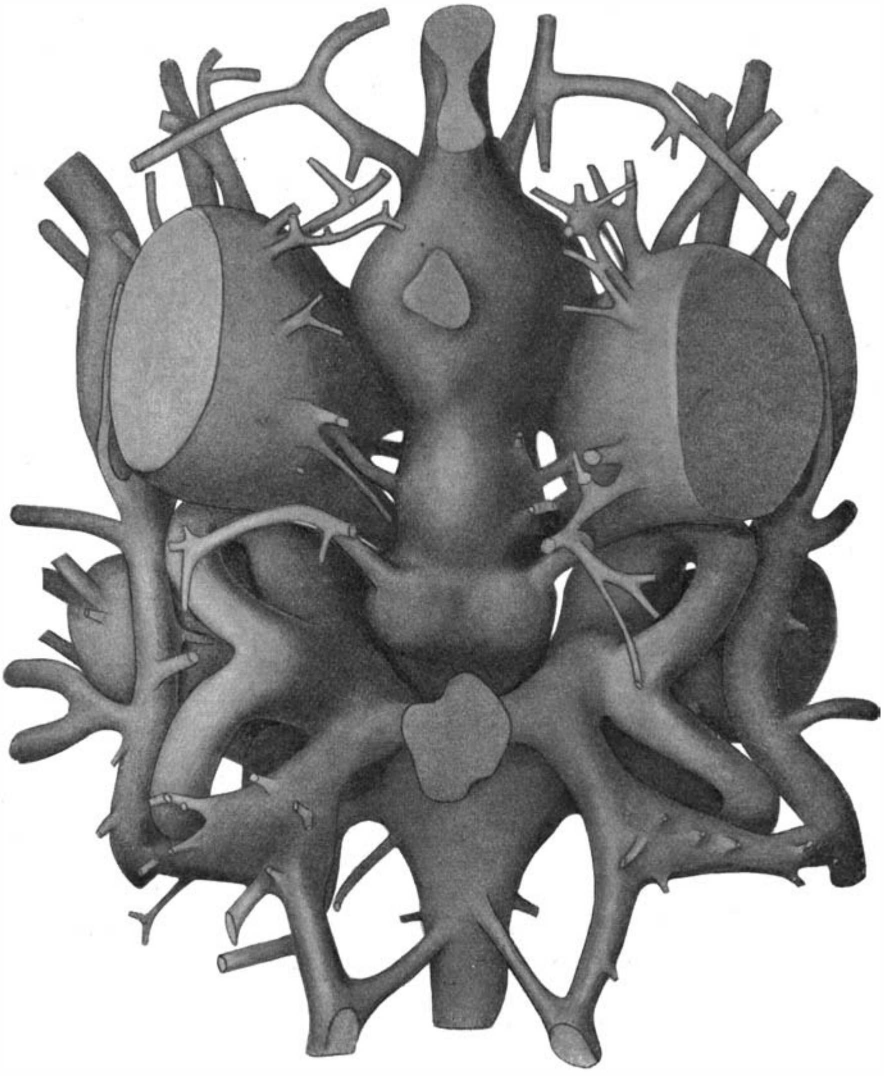
a. sa, canal for the first (anterior) dorso-lateral superficial artery; *a. sm*$_1$, canal for a dorso-lateral superficial artery, perhaps the dorso-lateral superficial artery 2; *a. sm*$_2$, canal for the dorso-lateral superficial artery 3; *ax*$_1$, *ax*$_2$, canals to the dorsal parts of the dorsal wall of the endocranium, probably for arteries; *bu*$_1$, *bu*$_2$, canals for branches from the n. buccalis lateralis and perhaps also for general cutaneous branches; *com*, commissural division of the labyrinth cavity; *c. sem. ant*, division of the labyrinth cavity for the canalis semicircularis anterior; *c. sem. post*, division of the labyrinth cavity for the canalis semicircularis posterior; *d*$_1$, opening leading to the very lateral margin of the dorsal electric field, probably for the ductus endolymphaticus and in addition for a vein; *des*, canal for the nerve to the dorsal electric field; *dic*, division of the cavum cerebrale for the diencephalon; *dsf*, portion of the dorsal electric field (deepest portion in which the two canals *des* unite); *ex*, small canal perhaps for a vessel; *f. opt*, optic fenestra; *mec*, division of the cavum cerebrale for the mesencephalon; *med*, division of the cavum cerebrale for the medulla oblongata; *met*, division of the cavum cerebrale cranii for the metencephalon; *my*, myodome; *na*$_1$, opening of the hypophyseal sac; *na*$_2$, nasal opening proper; *nd*$_1$, canal for the myelonal vein 1 and probably also for the dorsal root of the spino-occipital nerve 1; *nd*$_2$, canal for the myelonal vein 2 and probably also for the spino-occipital nerve 2; *nv*$_1$, canal for the ventral root of spino-occipital nerve 1 and in addition also for the myelonal artery 1; *olfc*, postero-dorsal part of the ethmoidal cavity occupied by the olfactory organ; *orb*, orbit; *pin*, pineal canal; *sel*$_{1,2}$, common canal for the first and second nerves to the lateral electric field; *sel*$_3$, canal for the third nerve to the lateral electric field; *tel*, division of the cavum cerebrale for the telencephalon; *v. cl*, canal for the vena capitis lateralis; *v. cl*$_1$, canal for the preorbital portion of the vena capitis lateralis; *vd*$_1$, vein canal leading to the orbit; *v. ds*, canal for veins from the dorsal parts of the otic region; *v. dsv*, canal for the otical vein and in addition probably for the ductus endolymphaticus; *vest*, vestibular division of the labyrinth cavity; *v. la*, canal for a lateral tributary to the vena capitis lateralis formed by the confluence of the dorso-lateral superficial veins 3 and 4; *v. lp*, canal for a lateral tributary to the vena capitis lateralis formed by the confluence of the dorso-lateral superficial veins 5 and 6; *v. lab*, canal for a vein or a nerve from the vestibular division of the labyrinth cavity or for both; *v. ls*$_1$, *v. ls*$_2$, *v. ls*$_5$, *v. ls*$_6$, canals for the dorso-lateral superficial veins 1, 2, 5, and 6 respectively; *v. so*$_1$—*v. so*$_4$, canals for veins from the surroundings of the nasal opening and the dorsal side of the interorbital wall; *vs. oc*, occipital vein sinus; *vv. sup*, canals for superficial veins to the occipital vein sinus; *vy*, canal for a vessel; III, canal for the n. oculomotories; IV, canal for the n. trochlearis; *V*$_1$, canal for the n. profundus; *V*$_2$, canal for the n. trigeminus proper; *VII+a. sa*, canal for the n. facialis and for a dorso-lateral superficial arterial trunk, certainly the first dorso-lateral superficial artery; X*vcp*, branch from the vagus canal for the vena cerebralis posterior.

Finally, the third branch goes always antero-laterally on the part of the visceral endoskeleton situated between the canals for the n. profundus and the n. trigeminus proper (*a. am*, text-figs. 44, 46, 47, 49; pls. 27, 29, 30, 39; pl. 40, fig. 5; pl. 55). With its distal part it entered the lateral electric field. It will be called the mandibular branch.

From the position and mode of branching of its canal, therefore, we find that the arteria facialis arose from the carotid artery and that it carried blood to the subaponeurotic vascular plexus of the upper surface and the interior of the part of the cephalic shield situated in front of the facialis nerves of both sides, save the dorsal parts of the interorbital wall behind the pineal canal. It is also evident that this artery gave off branches with a certain metameric disposition. As we thus see it was in all important features so similar to the arteria facialis of *Petromyzon* that it undoubtedly must have been homologous with that (cf. CORI, 1906, pp. 33—34, pls. XI, XII; HATTA 1922, pp. 142—150).

The vein canals of the region still remain to be considered. And among them we shall first turn to the canal $v. cl_1$, which as has already been pointed out above, lodged the preorbital portion of the vena capitis lateralis. This canal arises by the confluence of several fine branches from the subaponeurotic vascular plexus of the anterior parts of the region medially to the canal for the n. profundus and from the same vascular plexus of the rostral part of the visceral endoskeleton (text-figs. 23—25, 27, 28, 46, 47, 49—51; pls. 21, 27, 28, 29; pl. 40, fig. 5; pl. 45; pl. 47, fig. 1; pls. 49, 50, 55). It then goes backwards on the dorsal surface of the region medially or dorso-medially to the canal for the n. profundus (V_1), finally penetrating into the interior of the region and, as we have seen, opening into the orbit somewhat dorso-medially to the canal for the n. profundus. Only in *C. vogti* — in the specimen figured in pl. 27 — it makes during its course backwards a bend laterally, so that for a certain stretch it becomes situated laterally to the canal for the n. profundus (V_1), posteriorly to that stretch, however, occupying again its normal position in relation to the said nerve canal. Accordingly in the specimen of *C. vogti* just referred to it crosses the profundus canal at two points, at the anterior one of which it is coalesced with that canal (text-fig. 47).

Into the posterior part of the canal $v. cl_1$ there open several both lateral and medial branches. The most important of the lateral branches is the one lettered $v. sl_2$ in the figures (text-figs. 46, 47, 49, 50, 51; pls. 27, 28—30, 39, 45; pls. 49, 50, 55), which, with its most distal branches, arises from the lateral electric field from which it passes postero-medially on the dorsal (external) surface of the visceral endoskeleton, more exactly on the portion of this situated between the canals for the n. profundus and the n. trigeminus proper, receiving several twigs from its surroundings. Continuing postero-dorsally it finally enters



Text-fig. 27 B. *Kiaeraspis auchenaspidoides.* Cast of the cranial cavity, the labyrinth cavity, the orbits and the canals related to these cavities from the dorsal side. After a model in wax made after section series D. Magnification 23/1.

the ethmoidal region and opens into the canal $v.\,cl_1$, sometimes rather far anteriorly (*Kiaeraspis*, *Hoelaspis*, certain *Cephalaspis*-species), sometimes, on the contrary, far back close in front of the orbit (*Cephalaspis heintzi*). In the specimen of *C. vogti* figured in pl. 27 it opens into the part of the canal $v.\,cl_1$ that is situated laterally to the canal for the n. profundus. Moreover in this specimen it is considerably thicker and stronger than the part of the canal $v.\,cl_1$ situated in front of it, forming in fact the straight anterior continuation of the part of that canal situated behind it. From its course and position it is easy to see that it must be a serial homologue of the canals $v.\,ls_3$—$v.\,ls_6$ further back and that it accordingly lodged a dorso-lateral superficial vein. Since the anterior part or at least one of the lateral branches of the anterior part of the canal $v.\,cl_1$ may represent the first latero-superficial vein canal the one here in question ($v.\,ls_2$) seems to be the second one counted from in front.

The medial branches which open into the posterior part of the canal $v.\,cl_1$ come from the parts of the region laterally to the nasal aperture and from the posterior portions of the rostral part of the visceral endoskeleton (text-figs. 46, 47, 49, 50, 51; pl. 39, 41, 45; pl. 47, fig. 1; pls. 49, 50). The venous blood from the most postero-dorso-medial parts of the region, the posterior part of the circumnasal fossa and its surroundings, however, went to the orbit through the anterior supraorbital vein canals ($v.\,so$, $v.\,so_1$—$v.\,so_4$; text-figs. 27, 49; section series D, nos. 35—49; pl. 39).

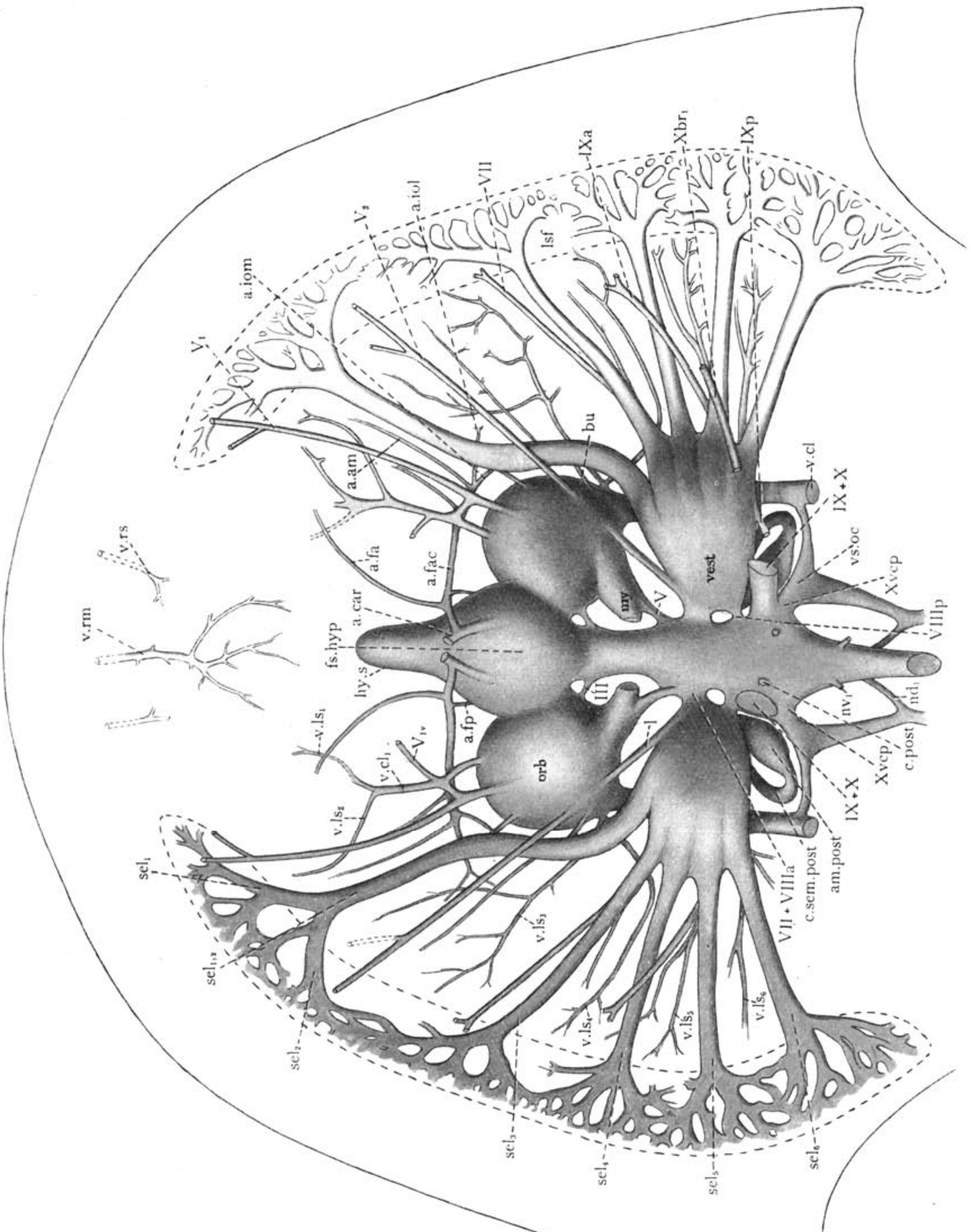
The posterior part of the canal $v.\,cl_1$ may in certain cases (pl. 28) be very wide and be provided with a distinct swelling close in front of the orbit. Concerning the posterior part of this canal is further to be noticed that in several specimens of *Cephalaspis hoeli* and in the specimens studied in detail of *C. vogti* and *Kiaeraspis* there is a communication between it and the profundus canal (V_1). In *C. hoeli* (text-figs. 23—25; section series A, nos. 130—152; section series B, nos. 56, 57; the specimen figured in pl. 21 seems, however, to have the two canals quite without anastomosis) and in *C. vogti* this communication takes place in the way that the two canals for a certain distance are united with each other while, on the contrary, in *Kiaeraspis* it arises in the way that they are connected by a more or less long cross-commissural canal, which at least in certain specimens continued even on the medial side of the canal $v.\,cl_1$, opening into the dorsal part of the oralo-branchial chamber (V_{1v}, text-fig. 28; pls. 49, 50; section series D, nos. 12—14, 18—21). From these conditions it seems very likely that a medial branch was given off from the n. profundus to the canal $v.\,cl_1$. But while this branch in most cases probably consisted only of general cutaneous fibres for the dorso-medial part of the upper surface of the ethmoidal region and the adjacent parts of the upper surface of the visceral endoskeleton it may perhaps in *Kiaeraspis* in addition have been composed of communis fibres, which, through the branch lettered V_{1v}, could have entered the oralo-branchial chamber. These supposed communis fibres would, of course, have formed a visceral ramus of the n. profundus; and we thus find that besides in *Hoelaspis* there are also in other forms certain facts which seems to point to that the n. profundus too had a visceral ramus. It does not seem improbable that the canal lettered V_{1v} of the *Kiaeraspis*-specimen just under consideration in addition to the supposed visceral nerve branch may very well be imagined to have been traversed by a small vein, forming a tributary to the preorbital portion of the v. capitis lateralis. And it is also possible, of course, that the said canal was traversed solely by such a vein. To decide positively what is correct in such a question as this is not possible.

Besides the canals described in the region there is in the specimen of *Kiaeraspis* used for section series D yet another one which has been found so far only on the right side. This canal (*ex*, text-fig. 27, section series D, nos. 15—21), which is very fine, leaves the right orbit medially to the canal $v.\,cl_1$ and goes antero-dorso-medially. It could not be followed to its termination, but it seems not improbably that it lodged a vessel.

Cavum cerebrale cranii and brain. — The cavum cerebrale cranii (text-figs. 15—17, 20—28; section series A; section series B; section series C, nos. 1—40; section series D, nos. 1—34; pl. 13, fig. 3; pl. 14; pl. 19, fig. 3; pls. 21, 28, 45; pl. 47, fig. 1; pls. 48, 49, 55) is well developed, and in all forms in which it is known so far it has a rather complicated shape. In several of the forms, particularly in the Silurian ones it was lined by a perichondral bone-layer, the internal perichondral bone-layer as it is called in this work (cf. pp. 30—31 above).

In its present state of preservation the cavum cerebrale cranii is, as we have found (pp. 124—125 above), continuous anteriorly with the ethmoidal cavity which lodged the olfactory organ and the anterior part of the hypophyseal sac; but in the living forms it was certainly separated from the dorsal parts of that cavity by a thick membrane of connective tissue. How I imagine this membrane to have been situated is shown in text-fig. 32 (*mbr*). Attention should here also be called to the fact that the ethmoidal cavity is lined by the internal perichondral bone-layer, when this is present.

Among the Spitsbergen material now available the cavum cerebrale cranii has been studied in detail in *Cephalaspis hoeli* and in *Kiaeraspis*, and where nothing is stated to the contrary the account given of it below is based entirely on these two forms. It deserves to be added, however, that the cavum cerebrale, from what is known of it in a number of other forms, must have been very similarly shaped as a whole in all Cephalaspids.



Text-fig. 28. *Kiaeraspis auchenaspidoides.*

Text-fig. 28. *Kiaeraspis auchenaspidoides.* Cast of the cranial cavity, the orbits, the labyrinth cavities and certain canals. Ventral aspect. Restored after the specimens figured in pls. 49, 50, 51 and 55. $^{12}/_{1}$.

a. am, mandibular branch of the facial artery; *a. car*, canal for the carotid artery; *a. fa*, anterior branch of the canal for the facial artery; *a. fac*, canal for the facial artery; *a. fp*, canal for a dorso-posterior branch of the facial artery; *a. iol*, lateral infraorbital branch of the canal for the facial artery; *a. iom*, medial infraorbital branch of the canal for the facial artery; *am. post*, swelling for the ampulla posterior; bu_1—bu_8, canals probably for branches from the n. buccalis lateralis and perhaps also for vessels; *c. post*, canal for the posterior encephalic artery; *c. sem. post*, division of the labyrinth cavity for the canalis semicircularis posterior; *fs. hyp*, fossa hypophyseos; *hy. s*, division of the cranial cavity for the hypophysial sac; *l*, canal for the lateralis fibres to the trigeminus-profundus ganglionic complex; *lsf*, lateral electric field; *my*, myodome; nd_1, canal for the myelonal vein 1 and in addition probably for the dorsal root of the first spino-occipital nerve; nv_1, canal for the ventral root of the spino-occipital nerve 1 and in addition for the myelonal artery 1; *orb*, orbit; $sel_{1,2}$, common canal for the two most anterior nerves to the lateral electric field; sel_1—sel_6, canals for the nerves to the lateral electric field; *v. cl*, canal for the vena capitis lateralis; $v.\,cl_1$, canal for the preorbital portion of he vena capitis lateralis; *vest*, vestibular divison of the labyrinth cavity; *v. la*, canal for a lateral tributary to the vena capitis lateralis formed by the confluence of the dorsolateral superficial veins 3 and 4; *v. rm v. rs*, canals for rostral veins; $v.\,ls_1$—$v.\,ls_6$, canals for the dorso-lateral-superficail veins 1—6; *vs. oc*, occipital vein sinus; III, canal for the n. occulomotorius; V, canal for the trigeminus roots (here only the division for the viscero-motor root seen). V_1, canal for the n. profundus; V_2, canal for the n. trigeminus proper; $\mathrm{V}_{1\,v}$, canal perhaps for the supposed visceral branch of the n. profundus; VII, canal for the passage of the n. facialis from the orbit to the oralo-branchial chamber; VII+VIII*a*; acustico-facialis canal; VIII*p*, canal for a posterior branch of the n. acusticus; IX*a*, canal for the exit of the n. glossopharyngeus from the labyrinth cavity; IX*p*, canal for the entrance of the n. glossopharyngeus into the labyrinth cavity; IX+X, glossopharyngeus-vagus branch of the vagus canal; $\mathrm{X}_{\mathrm{br}1}$, canal for the first branchial branch of the n. vagus; X*vcp*, branch of the vagus canal for the vena cerebralis posterior.

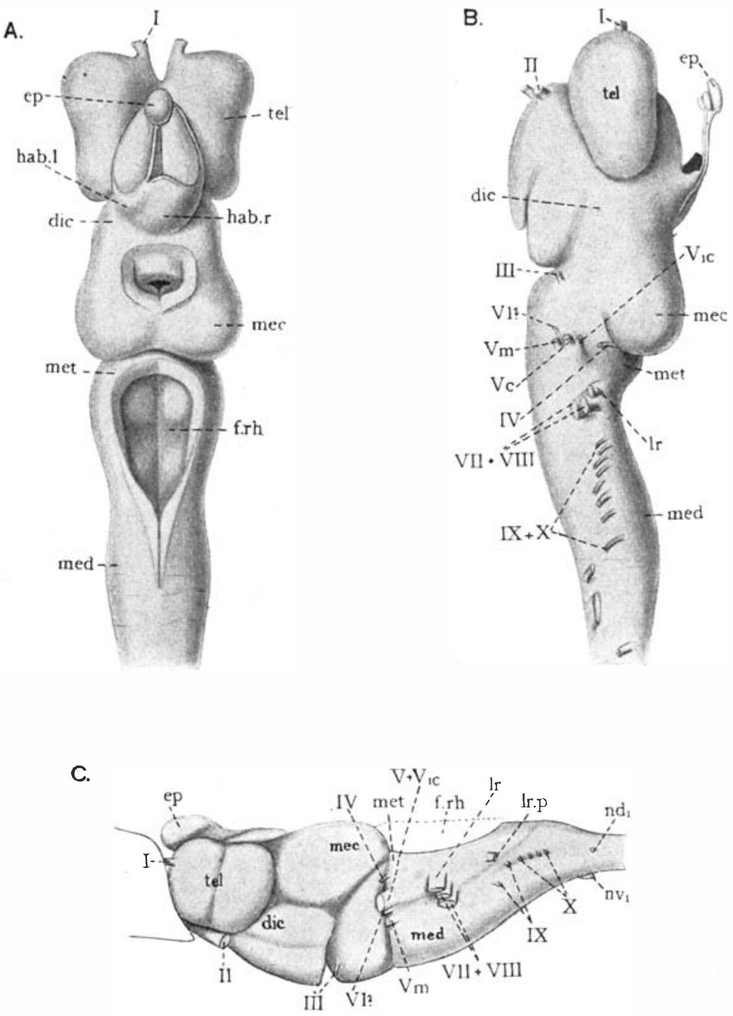
For the detailed description we may consider the cavum cerebrale cranii to consist of three divisions, which for the sake of brevity will be referred to simply as the posterior, middle and anterior divisions respectively.

The posterior one of these divisions (*med*, text-figs. 15—17, 20—28; section series A, nos. 12—63; section series C, nos. 1—40; section series D, nos. 2—29; pls. 14, 18; pl. 19, fig. 1; pl. 23, fig. 3; pls. 25, 26, 44, 45, 48, 49, 53, 54, 55, 57) constitutes the part of the cavum cerebrale that is situated in the occipital region and in a very short posterior part of the otic region posteriorly to the acustico-facialis canal (VII+VIII*a*), being in the latter region very well marked off from the middle division by its smaller height. It may vary rather much in length according to the length of the occipital region. Posteriorly it is hardly more than a rather fine tube which is somewhat higher than broad (section series A, nos. 12—39; section series D, nos. 13—25; pls. 23, fig. 3); and, as far as can be judged, it thus has there approximately the same diameter as the spinal canal. Forwards, somewhat behind the vagus canal, it rapidly commences to increase both in height and width, particularly, however, in width, soon attaining a width which is between two and three times as great as that at the posterior end. Finally most anteriorly at the transition to the middle division it becomes slightly lower and narrower again. On account of the asymmetric position of the aortal groove the bottom of the division may often be somewhat asymmetrical (text-figs. 16, 21, 24, 26; section series A, nos. 13—63; section series B, nos. 1—18; section series D, nos. 1—9). From the division issue: in the posterior narrow part the canals for the roots of the spino-occipital nerves (nd_1, nv_1, nd_2, nv_2), which, as we have seen, alternate with each other on both sides and which vary in number in different forms according to the length of the occipital region; in the anterior wide part the very high vagus canal (IX+X+X*vcp*), the canal for the posterior branch of the n. acusticus (VIII*p*), the canal *dx*, the canal for the occipital encephalic artery (*c. post*) and sometimes (*C. hoeli*) an additional fine canal (*t*) above the one for the posterior branch of the n. acusticus. These nerve canals show quite clearly that the division must have lodged the chief part of the medulla oblongata but that the anterior part of that had its position within the division in front.

The middle division may be considered to stretch from the posterior border of the acustico-facialis canal (VII+VIII*a*) forwards to the dorsum sellae, that is to say, to the posterior end of the fossa hypophyseos (*met*, *med*, *mec*, text-figs. 15—17, 20—28, section series A, nos. 63—99; section series B, nos. 19—38; section series C, nos. 1—38; section series D, nos. 2—33; pl. 13, figs. 2, 3; pl. 14; pl. 19, fig. 1; pls. 26, 45; pl, 47; fig. 1; pls. 48, 49, 55). It is somewhat lower anteriorly than in its middle and posterior parts, but its height is nevertheless throughout much greater than that of the posterior division. With regard to width it equals in the posterior part the posterior division, forwards, however, getting somewhat narrower than that. It is composed of three sub-divisions.

One of these sub-divisions constituted the postero-ventral part of the division in question, forming the direct anterior continuation of the posterior division. Its height, which somewhat exceeds one half of the total height of the division at this place is considerably less than the width and the length. From this sub-division there issue most postero-ventro-laterally the acustico-facialis canal (VII+VIII*a*) and in the antero-lateral or antero-ventro-lateral part either the canal for all the trigeminus-profundus roots, as in *Kiaeraspis*, or the two canals (V*c*, V*d*) for the roots of the trigeminus proper, as in *Cephalaspis*, and most other forms. And hence it is obvious that it must have lodged the anterior part of the medulla oblongata.

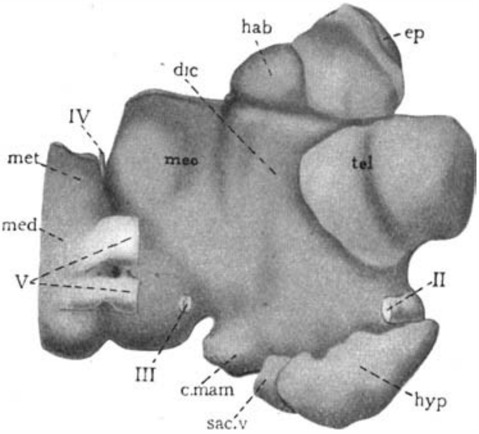
The sub-division to be dealt with next is the one lettered *met* in the figures. With regard to its proportions it is noticeable that this subdivision is rather short, shorter than the other two. On the contrary



Text-fig. 29. Brains of two petromyzontids. A and B of *Petromyzon fluvialtilis* in dorsal and lateral views. After AHLBORN 1884. C of *Petromyzon wilderi* from JOHNSTON 1902.

dic, diencephalon; *ep*, epiphysis; *f. rh*, fossa rhomboidalis; *hab. l*, left ganglion habenulae; *hab. r*, right ganglion habenulae; *lr*, root of the lateralis nerves accompanying the prootic nerves; *mec*, mesencephalon; *med*, medulla oblongata; *met*, cerebellum; nd_1, dorsal root of the first spino-occipital nerve; nv_1, ventral root of the first spino-occipital nerve; *tel*, telencephalon; I, olfactory nerve; II, optic nerve; III, n. occulomotorius; IV, n. trochlearis; $V+V_{1c}$, general cutaneous root of the n. profundus and the n. trigeminus; V*c*, general cutaneous root of the n. trigeminus; V*m*, viscero-motor root of the n. trigeminus; V_{1c}, general cutaneous root of the n. profundus; VI? n. abducens?; VII+VIII, acustico-facialis roots; IX, roots of the glossopharyngeus; IX+X, roots of the n. glossopharyngeus and the n. vagus; X, roots of the n. vagus.

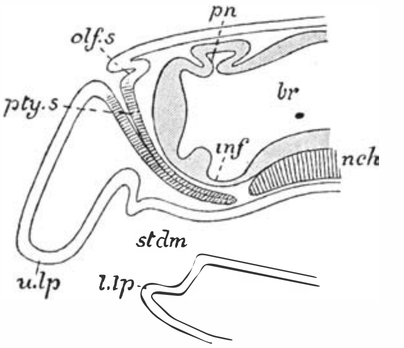
it is somewhat broader than these; and owing to this fact it appears very distinctly marked off from them. Dorsally it is distinctly bilobated. From its antero-dorso-lateral corner the canal *a. dsm*, which we have found to be an arterial canal (p. 73) and to have lodged the post-orbital superficial artery, goes out to the dorsal surface of the neuro-cranium. The sub-division in question certainly lodged the cerebellum, which must have been rather well developed and probably bilobated in the dorsal parts. Finally the third sub-division — lettered *mec*, in the figures — which follows anteriorly to the sub-division just described constitutes the entire anterior part of the division. It is somewhat narrower than the two other sub-divisions and in addition also somewhat lower than these two together. Generally it is marked off from the cerebellar sub-divison (*met*) by a narrowing, which, however, sometimes may be rather indistinct. At the middle of the length, or somewhat behind that, it is always somewhat wider than anteriorly and posteriorly. and at the same time it has at this place also a more or less distinct dorsal bulge. Its maximum width is almost equal to the length and both the maximum width and the length are somewhat less than the maximum height. The maximum height is situated at the transition to the posterior two sub-divisions, diminishing forwards by the gradual raising of the bottom. From the sub-division in question there issue regularly the canal for the n. trochlearis (IV), the canal for the n. oculomotorius (III) and the canal for the supposed pituitary vein (*v. pt*) and in addition — in many cases, as in *Cephalaspis hoeli* and certain other forms — also the two canals (V*a*, V*b*) for the roots of the n. profundus. The canal for the n. trochlearis leaves the subdivision high up more or less close in front of the transition to the sub-division for the cerebellum (*met*), in *Cephalaspis hoeli* together with the canal (V*b*) for the general cutaneous root of the n. profundus. The canal for the n. oculomotorius goes out from the lower half of the most anterior part of the sub-division either straight above or at a transversal plane not very far behind the dorsum sellae, while the canal for the supposed pituitary vein (*v. pt*) takes its origin from the bottom of the sub-division either at or behind the middle and thus rather far back. Finally in *Cephalaspis hoeli* the remaining one (V*a*) of the two canals for the roots of the n. profundus — the canal for the supposed viscero-motor root of the n. profundus — leaves the sub-division in the lower half approximately at the middle of the length and somewhat antero-ventrally to the canal for the general cutaneous root of the same nerve. It deserves also to be mentioned in this connection that certain fine canals (ax_1, ax_2), which probably transmitted arteries, issue from the dorso-lateral parts of the region more or less close to the trochlearis canal. As is seen from its position and from the nerve canals issuing from it, the sub-division in question must have lodged the mesencephalon, which thus was well developed and rather long.



Text-fig. 30. *Ichthyomyzon concolor.* Anterior parts of brain in lateral view, from HERICK & OBENCHAIN 1913.

c. mam, corpus mammillare; *dic*, diencephalon; *ep*, epiphysis; *hab*, right habenular ganglion; *hyp*, hypophysis; *mec*, mesencephalon; *med*, medully oblongata (anterior part); *met*, cerebellum; *sac, v*, saccus vasculosus; *tel*, telencephalon; II, n. opticus; III, n. oculomotorius; IV, n. trochlearis; V, roots of the n. trigeminus proper and of the n. profundus.

The anterior division (*tel*, *dic*, text-figs. 15—17, 20—25, 27, 28; section series A, nos. 100—134; section series B, nos. 39—48; section series C, nos. 1—40; section series D, nos. 1—34; pl. 13; figs. 2, 3; pls. 14, 21, 28, 45; pl. 47; fig. 1; pls. 48, 49, 55) of the cavum cerebrale stretches from the dorsum sellae forwards to the ethmoidal cavity and is regularly shorter than the other divisions, but on the other hand higher and in certain cases also broader than these. It is well marked off both posteriorly towards the middle division and forwards towards the ethmoidal cavity. The height is generally its greatest, the length its smallest dimension. The maximum width is situated in its antero-ventral part. Its ventral part, which forms a wide and long fossa hypophyseos (*fs. hyp*), lies much lower than the dorsum sellae, being with its floor approximately in a level with the orbital floor (section series B, nos. 39—44). In the fossils the division is in open communication with the orbit of each side, by the wide optic fenestra (*f. opt*) but in the living forms, as has been pointed out above,the optic fenestra was certainly closed by a membrane of connective tissue. The roof of the division is pierced by the wide pineal canal (*pin*), which, as we have seen, opens outwards on the dorsal side of the neurocranium rather close behind the nasal aperture. Anteriorly to that canal the division may, as in the specimen of *Cephalaspis hoeli* used for section series A (text-figs. 15, 17; section series A, nos. 113—116) be imperfectly divided dorsally into a right and a left half by a sagittally running median ridge of the roof. On the posterior side of the pineal canal and in connection with it we find in addition, in the specimen of *C. hoeli* just referred to, a distinct bulge (*hab*, *hab.r*, text-figs. 15, 17, 23; section series A, nos. 99—101) on the dorsal side of the division, a bulge which is somewhat asymmetric, being situated somewhat more to the right than to the left side. This bulge evidently lodged the habenular ganglia, which must have been large and asymmetrically developed, in the same way as in the recent *Petromyzon*



Text-fig. 31. *Petromyzon.* Diagram of a larval stage, showing the extension and shape of the olfactory and hypophyseal sacs. From PARKER & HASWELL 1910 (altered from DOHRN).

br, brain; *inf*, infundibulum; *l. lp*, lower lip; *nch*, notochord; *olf. s*, olfactory sac; *pn*, epiphysis; *pty. s*, hypophyseal sac; *stdm*, stomodaeum; *u. lp*, upper lip.

(cf. text-figs. 29, 30). In certain forms such as *Boreaspis rostrata* (pl. 13, figs. 2, 3) and *Hoelaspis* (pl. 47, fig. 1) there is a distinct ridge[1] on the roof of the division which has the shape of a V with the point forwards close anteriorly to the pineal canal and the opening backwards; and, as far as I can judge, this ridge markes the boundaries between the dorsal parts of the diencephalon and telencephalon, both of which thus dorsally had a similar extent and shape as in the Petromyzontids (cf. text-figs. 29, 30). The n. opticus emerged into the orbit through the fenestra optica and thus, in the living forms, after having pierced the membrane which closed that fenestra, while the n. olfactorius, which certainly was paired, pierced the dorsal half of the membrane that separated the division from the ethmoidal cavity. The carotid artery, which, as we have seen, was paired, entered the fossa hypophyseos rather far antero-laterally close medially to the anterior part of the fenestra optica. From everything known so far it is easy to see that the division lodged the diencephalon and the telencephalon and that the latter certainly only occupied the antero-dorsal part of it. Since, as we have found, (cf. pp. 124—125 above) the antero-ventral division of the nasal aperture leads to the fossa hypophyseos it is evident, as has already been pointed out, that the hypophyseal sac extended backwards into that fossa and was situated there beneath the hypophysis. And, as we have also seen, the hypophyseal sac must have ended blindly in the fossa hypophyseos. It was thus even less long than in the adult *Petromyzon* and may probably have been approximately as in the larval stage of *Petromyzon* shown in text-fig. 31.

As may easely be understood from the figures and from the statements given, the cavum cerebrale cranii cannot have been very much wider than the brain and it is therefore obvious that it reflects at least the main features of this. We are thus able to conclude that the oblongata was broad and strongly developed, that probably there was a bilobated

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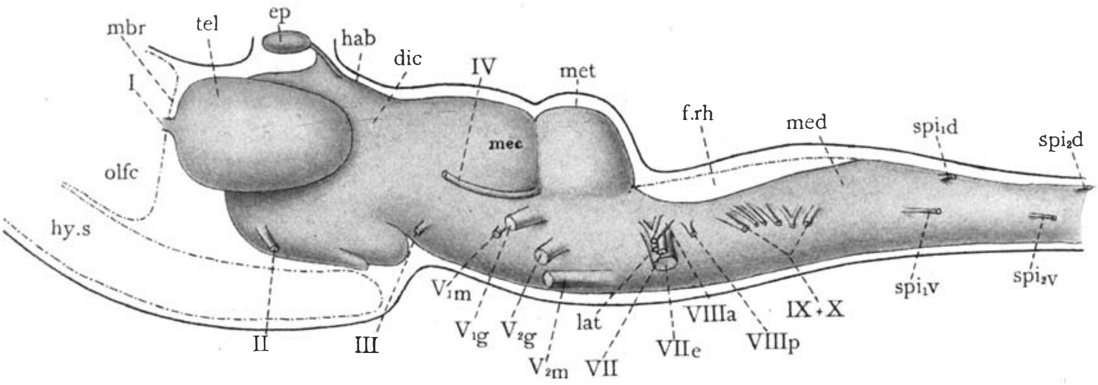
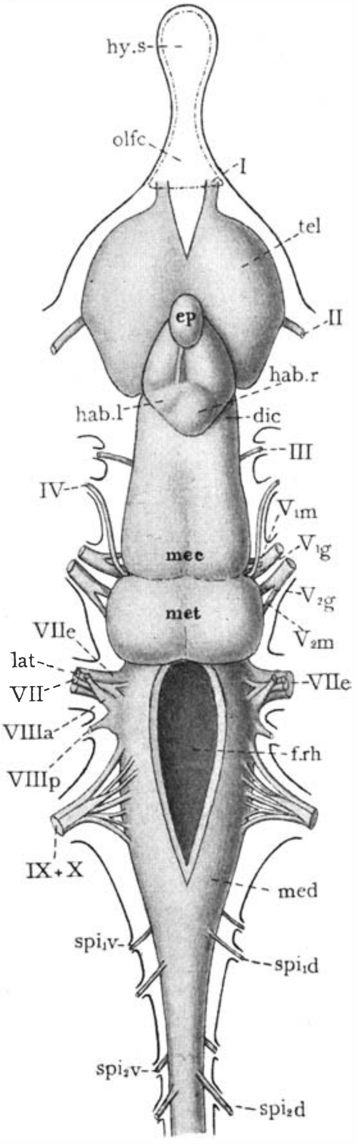
[1] In the figures quoted this ridge is only represented by an impression and therefore it appeares as a groove.



Text-fig. 32 A. Attempted restoration of the brain of *Kiaeraspis* in lateral view. Outlines of the cavum cerebrale with a thick continuous line.

dic, diencephalon; *ep*, epiphysis; *fr. h*, fossa rhomboidalis; *hab*, habenular ganglia; *hab. l*, left ganglion habenulae; *hab. r*, right ganglion habenulae; *hy. s*, hypophysial sac; *lat*, root or roots of the prootic lateralis nerves; *mec*, mesencephalon; *med*, medulla oblongata; *mbr*, membrane of connective tissue separating the cavum cerebrale from the olfactory sac; *met*, cerebellum; *olfc*, cavity for the olfactory organ; $spi_1\ d$, dorsal root of the first spino-occipital nerve; $spi_1\ v$, ventral root of the first spino-occipital nerve; $spi_2\ d$, $spi_2\ v$, dorsal and ventral roots of the spino-occipital nerves 2; *tel* telencephalon; I, olfactory nerve; II, optic nerve; III, n. oculomotorius; IV, n. trochlearis; $V_1\ g$, general cutaneous root of the n. profundus; $V_1 m$, supposed viscero-motor root of the n. profundus; $V_2 g$, general cutaneous root of the n. trigeminus proper; $V_2\, m$, viscero-motor root of the n. trigeminus proper; VII, facialis roots; VII*e*, root or roots of the nerves to the electric fields; VIII*a*, anterior branch of the n. acusticus; VIII*p*, posterior branch of the n. acusticus; IX+X, roots of the n. glossopharyngeus and the n. vagus.



Text-fig. 32 B. Attempted restoration of the brain of *Kiaeraspis* in dorsal view. For the explanation of the index letters see the text-fig. 32 A.

rather large cerebellum, a rather long mesencephalon, somewhat wider posteriorly than anteriorly, a very high and strongly developed diencephalon, and, finally, a small paired telencephalon, which latter chiefly consisted of the olfactory centres and which was situated rather high up in the cavum cerebrale. From the facts known it is also easy to see that the brain must have been very like that in the Petromyzontids (text-figs. 29, 30, 32). In these, however, the cerebellum is very slightly developed; and in this respect, therefore, the Cephalaspids agree with *Myxine*, which has a rather large bilobated cerebellum (cf. text-fig. 42 in this work and HOLMGREN 1919, pp. 83—87). How I imagine the brain of the Cephalaspids to have been is shown by the attempted restoration given in text-fig. 32.

Visceral endoskeleton.

After the account given of the endocranium we shall next pass to the visceral endoskeleton.

The visceral endoskeleton consisted of two different divisions: a dorsal one, which as already pointed out, is continuous with the endocranium and forms part of the cephalic shield, and a ventral one which was situated in the soft tissue that closed the oralo-branchial fenestra and which was quite independent of the dorsal division and the cephalic shield. Whereas the dorsal division lies dorsally to the branchial openings and always is more or less completely ossified, the ventral division on the contrary had its position ventrally to the external branchial openings on the ventral side of the head and seems to have been entirely cartilaginous, a condition which had the result that it could not be preserved in the fossils. On account of the fact that the external branchial openings were rather small, of about a corresponding size relatively as in Cyclostomes, it is quite obvious that the dorsal and ventral divisions of the visceral endoskeleton, as here defined, represented approximately the dorsal and ventral halves respectively of the visceral endoskeleton. And we thus find that with regard to the relations between the size of the branchial openings and the length of the divisions of the visceral endoskeleton situated dorsally and ventrally to these openings, the conditions were not as in fishes but as in Petromyzontids.

Owing to its position in the ventral wall of the oralo-branchial chamber, that certainly was intensely moved and played an important part for the respiration, the ventral division must either have been a single thin big plate of some flexible sort of cartilage or have consisted of a number of small independent cartilaginous plates. That it could not have consisted of independent visceral arches is, as we shall find, definitely shown by the conditions of the dorsal division.

No further details can be ascertained concerning the ventral division; and as in the sequel we have no occasion to deal with that division any more but the entire account that follows is based solely on the dorsal division, this will for the sake of brevity be referred to simply as the visceral endoskeleton.

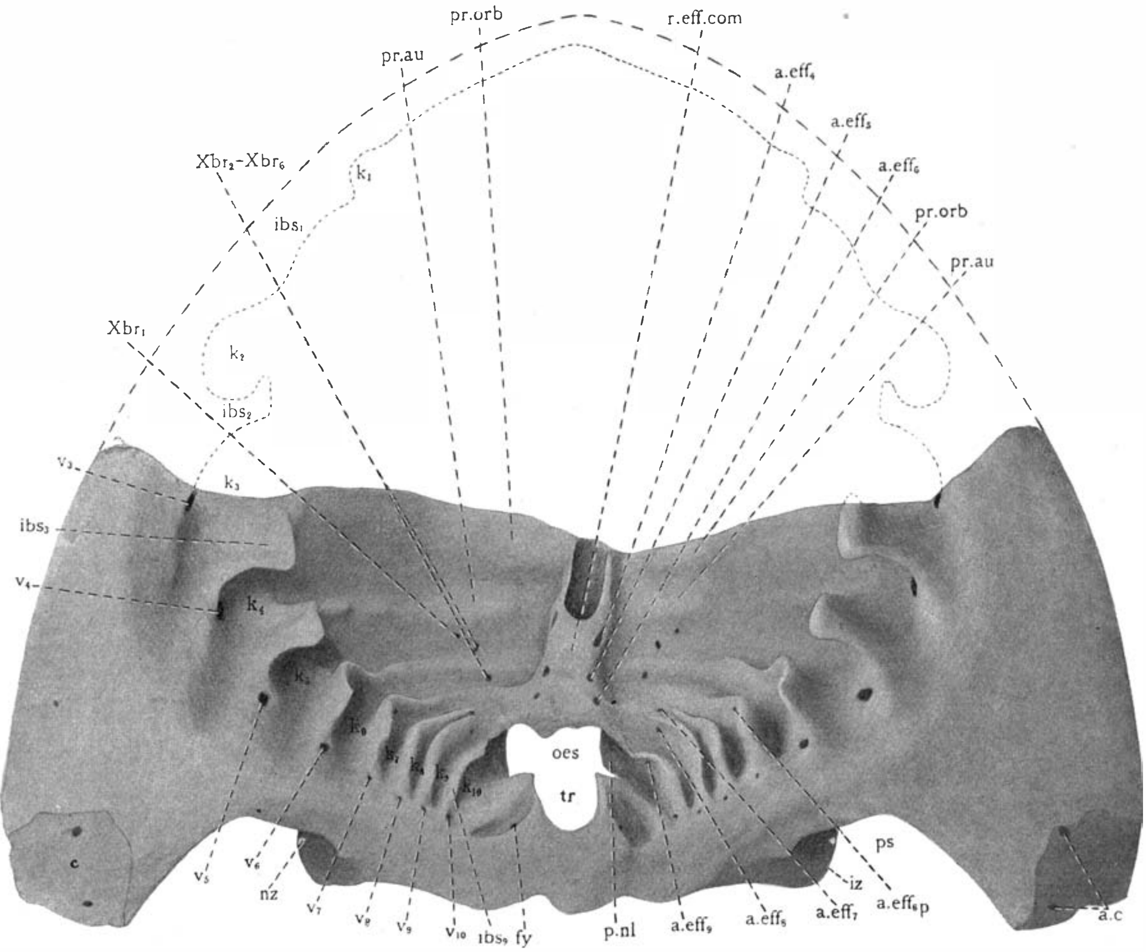
The visceral endoskeleton in this restricted sense (the dorsal division of the visceral endoskeleton) constitutes a considerable part of the endoskeletal component of the cephalic shield (text-figs. 2, 4, 8, 9—13, 33, 34, 36), forming not only the rostral but also the lateral and to a great extent also the postero-ventral portions of that component. And as has already been noticed, it bounds the oralo-branchial chamber anteriorly, laterally and posteriorly. Concerning its position special attention should be called to the fact that, as we shall find, it was situated between the subaponeurotic vascular plexus on the outside and the visceral musculature on the inside. Finally, it is also very noticeable, that, as is well displayed by certain of the figures (text-figs. 4, 13, 33, 34, 36; pls. 14, 15, 22, 44, 51, 52), it does not consist of independent skeletal bars but forms a continuous skeletal mass throughout its extension.

For the detailed discription we may consider the visceral endoskeleton to be composed of an unpaired rostral part, a paired lateral part and an unpaired posterior part, which has already been referred to as the postbranchial wall.

The rostral part forms the most anterior portion of the endoskeletal component of the cephalic shield, projecting in an antero-ventral direction from the anterior part of the ethmoidal region, with which it is continuous (text-figs. 2, 4, 7—13, 36; section series C; pls. 13—15, 27—29, 39, 44, 45, 46, 49—58). Though thicker in the median and antero-ventral portions than in its other ones, nevertheless, as a whole it is ather thin. According to the general configuration of the cephalic shield, it is curved so that in a direction transverse to the longitudinal axis of the head it is convex externally and concave towards the oralo-branchial chamber. And in those forms in which there was a rostral process it was probably produced so as to form the interior of that process, which otherwise consisted of exoskeletal bone. It presents two surfaces, an external and an internal one, the former of which is covered by the exoskeleton, while the latter is lined by the external perichondral bone-layer and forms the anterior surface of the oralo-branchial chamber. The external surface consists of two distinctly separated fields, an antero-dorsal one which for the sake of brevity will be referred to simply as the dorsal field, and a ventral one which constitutes the rostral part of the ventral rim of the endoskeleton. The internal surface has a rather complicated relief, to the details of which we shall return below.

The lateral part of the visceral endoskeleton of each side, if we next pass to that (text-figs. 2, 7—13; 33, 34, 36; section series B, nos. 1, 6; section series C, nos. 99—130; pls. 14, 15, 22, 44, 45, 49 -58), lies ventro-laterally to and passes over dorso-medially into the lateral parts of the ethmoidal, orbitotemporal and otic regions of the endocranium. Posteriorly it is continuous not only with the postbranchial wall but also with the endoskeletal shoulder-girdle. It is considerably thicker ventrally than dorsally, and as a whole it gets thicker backwards. Like the rostral part, it has an external and an internal surface, the former of which is covered by the exoskeleton, while the latter, which forms the lateral surface of the oralo-branchial chamber, is provided with a portion of the external perichondral bone-layer. The external surface is also — quite like that of the rostral part, with which it is continuous — composed of two fields, a latero-dorsal one, which will be called simply the dorsal one, and a ventral one, which represents the lateral part of the ventral rim of the endoskeleton. On the dorsal field of this surface we find the chief anterior part of the lateral electric field (*lsf*, text-fig. 2, 3, 9—12; section series A, nos. 156—167; section series B, nos. 1, 6; section series C, nos. 100—130). The details of the internal surface will be described below in another connection.

Finally the posterior part of the visceral endoskeleton — the postbranchial wall, as it has been called above, and as it will be termed in this memoir (*p. brw*, text-figs. 2 A, 4, 9—14, 33—35; section series A, nos. 157—158; section series C, nos. 1—112; section series E, nos. 1—12; section series F, nos. 1—65; pls. 8—10, 14, 15, 20, 22; pl. 23, figs. 1, 3; pls. 28, 33, 42; pl. 46, fig. 1; pl. 47, fig. 1; pls. 51—53; pl. 54, fig. 1; pl. 56, fig. 1; pls. 57, 58; pl. 62, fig. 1) — descends, as we have already seen, from the lower side of the endocranium in a postero-ventral direction and reaches as far downwards as to the part of the exoskeleton that is situated on the ventral side of the cephalic shield, just behind the oralo-branchial fenestra, in this way forming a complete septum between the oralo-branchial chamber and the abdominal region. More exactly, it issues from the lower side of the endoskeleton with its medial part at the transition between the occipital and otic regions and with each one of its lateral parts somewhat more anteriorly from the otic region below the vestibular division of the labyrinth cavity. It is thus situated further forwards with each one of its lateral parts than with its medial one and accordingly it is curved from one lateral side to the other, so that it has the concavity forwards and the convexity backwards. Laterally, on each side of the median line, it is continuous both with the lateral part of the visceral endoskeleton and with the endoskeletal shoulder-girdle. In its dorso-medial and ventro-lateral parts it is fairly thick, but otherwise and as a whole it is rather thin. On it may be distinguished an anterior surface, which faces antero-ventrally and constitutes the posterior



Text-fig. 33. *Cephalaspis hoeli.* Posterior half of the cephalic shield in ventral view. Restoration made after the section series F. $^6/_1$.

a. c, canals for branches of the cornual artery; *a. eff*$_4$—*a. eff*$_9$, canals for the efferent branchial arteries 4—9; *a. eff*$_6$p, canal probably for a posterior portion of the efferent branchial artery 6; *c,* cornu; *fy,* canal probably for a ventral longitudinal superficial vein; *ibs*$_1$—*ibs*$_3$, *ibs*$_9$, interbranchial septa 1, 2, 3, 9; *iz,* interzonal part of the cephalic shield; *k*$_1$—*k*$_{10}$, branchial fossae; *nz,* canal probably for a nerve to the pectoral fin; *oes,* oesophageal division of the foramen for the oesophagus and the truncus arteriosus; *p. nl,* bone lamella, which protected the pronephros from the lateral side; *pr. au,* otical prominence; *pr. orb,* orbital prominence; *ps,* pectoral sinus; *r. eff. com,* ridge which lodged the arteria branchialis efferens communis; *tr,* division for the truncus arteriosus of the common foramen for the oesophagus and the truncus arteriosus; *v*$_3$—*v*$_{10}$, canals for the ventral transversal superficial veins 3—10; X$_{br_1}$, canal for the first branchial branch of the n. vagus; X$_{br_2}$—X$_{br_6}$, canals for the remaining posterior branchial branches of the n. vagus.

surface of the oralo-branchial chamber, and a posterior surface, which faces postero-dorsally towards the interior of the interzonal part of the cephalic shield and which dorsally is continuous with the posterior surface of the otic region and the ventral surface of the occipital region. Both its surfaces are lined with the external perichondral bone layer.

As has been pointed out already in the general description given of the oralo-branchial chamber, the postbranchial wall was perforated in the medial part by the oesophagus and the truncus arteriosus. And as has also already been pointed out, the openings for these two structures (*oes*, *tr*) are in certain forms (*Boreaspis*, *Kiaeraspis*) well separated from each other, while in other forms (*Benneviaspis, Hoelaspis*, *Cephalaspis*) they have fused into a single big foramen, consisting of a dorsal wide division for the oesophagus (*oes*) and a ventral smaller division (*tr*) for the truncus arteriosus. With its most dorso-medial part the postbranchial wall bridges over the aortal groove on the ventral side, so that this groove for a certain stretch is transformed into a canal, the aorta-canal (*aort* or *aort. gr*, text-figs. 2, 14; section series B, nos. 1—4; section series C, nos. 17—53; pl. 42; pl. 46, fig. 1, pl. 47, fig. 1, pls. 51, 52, 53, 58).

The anterior surface of the postbranchial wall presents a relief of much interest; but for practical reasons a description of this relief will not be given until later. Instead we shall now turn to the posterior surface of the said wall. This surface (text-figs. 9—12, 14, 34, 35; section series B, C, E, F; pls. 9, 10, 14, 15; pl. 46, fig. 1; pl. 47, fig. 1; pl. 52; pl. 53, figs. 2, 3; pl. 58) is bounded on each lateral side from a big cavity (*vs. marg*) by a ridge (*r. subcl*), which, for reasons to be given bolow, will be called the subclavian ridge and which goes from above downwards and slightly laterally to the ventro-medial part of the endoskeletal shoulder-girdle (*p. sh*). Most dorso-medially the posterior surface under consideration has on each side of the posterior opening of the aorta-canal, as above defined, a more or less closed pit (X*gn*) for the vagus ganglionic complex and laterally to that just beneath the otic region a laterally running groove (*n. lg*), probably for the n. lineae lateralis. More ventrally on the surface, immediately laterally and dorso-laterally to the oesophagus foramen or its homologue when this foramen has fused with the truncus arteriosus foramen, there is a thin paired lamella (*p. nl*) which projects backwards and which, together with its fellow of the opposite side, forms a chiefly supraoesophageal space, open backwards and probably also dorsally. More exactly this lamella issues from the surface along a line running dorso-ventro-laterally in such a way that with its dorsal parts it is somewhat inclined towards its fellows of the opposite side and so that the supraoesophageal space is narrower dorsally than ventrally. Moreover this lamella is curved slightly towards the median line with its posterior part and has on its medial surface a number of chiefly transversal grooves which are somewhat irregular. The supraoesophageal space is, at least in those cases in which it is known in detail, imperfectly subdivided into a right and a left part by means or a short unpaired lamella (*p. nm*), which issues in a backward direction from the postbranchial wall dorsally to the oesophagus foramen or its homologue. As the last-mentioned lamella is not situated quite in the median line, but lies nearer to the right than to the left side of the supraoesophageal space, the right part of that space is less than the left one. Concerning this space it must also be added here that it is situated close ventrally to the occipital region and the aortal groove. From its position and its features, as we shall see (cf. the chapter on the pronephros below), it is fully certain that it must have lodged the pronephros, and on account of this it will in the sequel be referred to as the pronephros space, while the paired lamella that bounds it laterally will be termed the pronephros lamella. In *Cephalaspis hoeli* (text-figs. 34, 35; section series F, nos. 13—29) and in certain other forms too there is, on the posterior surface of the postbranchial wall close laterally to each pronephros lamella, a distinct angular groove (*a. fc*, *a. subcl*) which arises owing to the fact that certain of the canals — those lettered in the figures *a. fc* and *a. subcl*, which pierce the postbranchial wall — had their posterior wall imperfectly ossified at this place. In *Kiaeraspis* (pl. 53, figs. 2, 3) and *Hoelaspis* (pl. 47, fig. 1), on the contrary, a correspondingly situated groove seems to be entirely lacking, the posterior wall of the canals *a. fc* and *a. subcl* probably having in them been completely ossified. Moreover we find on the posterior surface of the postbranchial wall two shallow less developed grooves, lettered in the figures *a. pbrw* and *a. pbrw*$_1$, and in addition the openings of numerous canals.

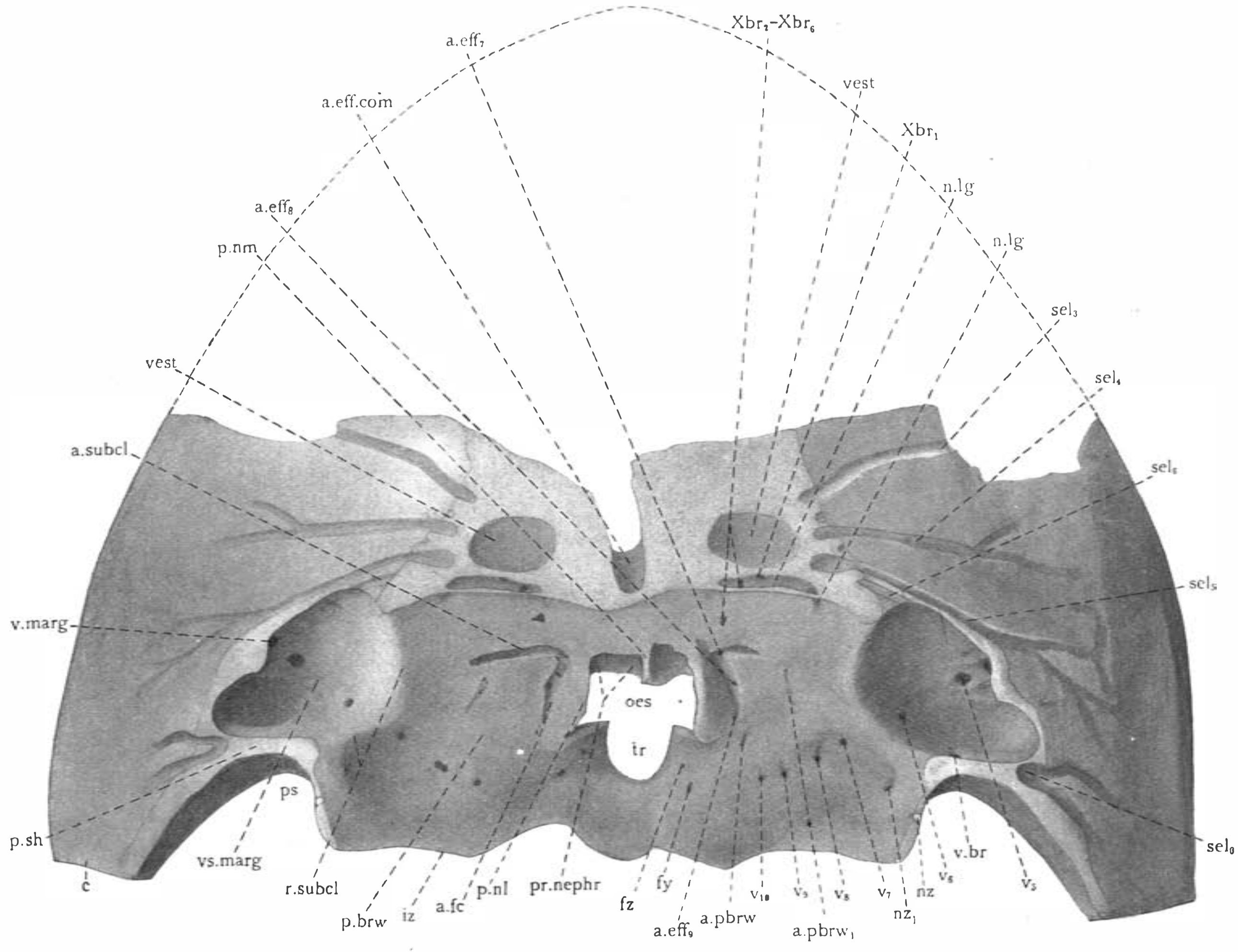
After this account of the general features of the different parts of the visceral endoskeleton and after having dealt in detail with the posterior surface of the postbranchial wall, we shall now turn to the internal surfaces of the rostral and lateral parts and the anterior surface of the postbranchial wall, that is to say the surfaces which bound the oralo-branchial chamber anteriorly laterally and posteriorly.

The internal surface of the rostral part (text-figs. 4, 9—13, 36; section series C; section series F, nos. 33, 39, 42, 45, 49; pls. 22, 44; pl. 46, fig. 1; pls. 51, 52; pl. 62, fig. 1) is in its dorso-medial — or, more correctly, postero-dorso-medial — part occupied by the most anterior portion of the aortal ridge (*r. aort*) with the likewise most anterior portion of the aortal groove (*aort. gr*). From the anterior end of the aortal ridge, a paired rather low but broad ridge, lettered in the figures *r. pm* (text-figs. 4, 36; pls. 44, 51), goes in an antero-latero-ventral direction to the ventral margin of the oralo-branchial chamber. On this ridge, for which the term prebranchial ridge will be employed there is in *Kiaeraspis* a rather fine but nevertheless very distinct groove (*a. rostr*) which leads backwards to the anterior end of the aortal groove and which, on account of that, must have been caused by an artery, which will be called the rostral artery. Owing to the fact that the prebranchial ridge of one side antero-ventrally diverges from its fellow of the other side, a triangular area (*dpr*, text-figs. 4, 9—13, 36; section series F, nos. 45, 49; pl. 40, fig. 4; pls. 44, 51; pl. 62, fig. 1), which is somewhat depressed or excavated, is formed between the two prebranchial ridges. And it is highly interesting to find that in *Thyestes verrucosus* this area is equipped with numerous small tubercles, which, as far as can be judged, consist of dentine and which certainly must be teeth. Here, therefore, we have a condition which enables us to conclude that the triangular area under consideration formed at least a part of the roof of the mouth cavity, and accordingly that the mouth cavity was situated far forwards beneath the rostral part of the cephalic shield. In addition to the structure dealt with we find on the internal surface of the rostral part of the visceral endoskeleton also the most dorso-medial portion of the first interbranchial ridge (ibr_1, text-figs. 4, 13, 36; pl. 44; pl. 46, fig. 1; pls. 51, 52), which reaches as far dorso-medially as the anterior end of the aortal ridge and which is provided with a distinct groove ($a.\ eff_1$) in its longitudinal direction. As this groove goes to the aortal groove and falls in the gill-bearing part of the head, it must beyond question have been caused by an efferent branchial artery — in fact, as will be further established below, by the first efferent branchial artery. Finally there are also on the internal surface in question the openings of several canals for nerves and vessels (V_1, *va*, *vs. r*, text-figs. 4, 13, 36).

Behind the prebranchial ridge there follow on the internal surface of each lateral part of the visceral endoskeleton and on the adjacent half of the anterior surface of the postbranchial wall the branchial fossae, which have already been partly dealt with above (p. 46) in the general description of the oralo-branchial chamber. These fossae (k_1—k_{10}, text-figs. 4, 9—13, 33, 36, 39, 40; section series C, nos. 85—123; section series F, nos. 10—61; pls. 14, 15, 22, 39, 44; pl. 46, fig. 1; pl. 51) could be studied completely only in *Cephalaspis hoeli* and in *Kiaeraspis*, in both of which they are found to be 10 in number. In the specimen of *Boreaspis rostrata* shown in pls. 14 and 15 there are also 10 to bee seen, but the most posterior one of these is situated so far laterally to the foramen (*tr*) for the truncus arteriosus that it may very well be imagined that in this form there were still one or two behind the 10th. It is certain, however, that, at least in the majority of Cephalaspids, they were exactly 10 and that in no Cephalaspid they can have exceeded 11 or 12.

The shape of the branchial fossae seems to vary somewhat in different forms (cf. pls. 15, 22, 51); but, as far as is known, they agree in all forms in being more wide and shallow in their dorsal and middle thirds than in their ventral third. Moreover they have also in common in all forms that in the most ventral part of their ventral third they rapidly become shallow again and that most ventrally they almost disappear, so that at the ventral border of the oralo-branchial chamber, thus at the medial margin of the ventral rim, they are hardly discernible any more (cf. text-fig. 33). Finally it is also to be noticed that all of them, or at least the 5—6 anterior ones, are curved so that their ventral third to a rather great extent lies in a transversal plane posteriorly to that of the middle and dorsal thirds (text-figs. 4, 33, 36, 39; pls. 15, 22, 44, 51), and that on account of this the interbranchial septa (ibs_1—ibs_9) too always lie in planes behind those of their corresponding interbranchial ridges (ibr_1—ibr_9).

The most anterior one — or, as it will be termed here, the first (k_1, text-figs. 4, 13, 33, 36; section series C, nos. 108—116; section series F, nos. 39, 42, 45; pls. 15, 44, 51) — of the branchial fossae follows immediately behind the prebranchial ridge and may be considered to be bounded by that anteriorly and by the interbranchial septum and interbranchial ridge 1 posteriorly. The interbranchial septum 1 (ibs_1) is, as a rule, broad but rather short. The interbranchial ridge 1 (ibr_1) continues, as we have found, so far medially as to unite with the anterior end of the aortal ridge. The branchial fossa following next backwards, i. e. the branchial fossa 2 (k_2, text-figs. 4, 13, 33, 36; section series C, nos. 109—124; section series F, nos. 39, 42, 45, 49; pls. 15, 22, 44, 51), which lies between the interbranchial septum and interbranchial ridge 1 anteriorly and the interbranchial septum and interbranchial ridge 2 posteriorly, is bigger than the first one, particulary in the ventral third. The interbranchial septum 2 is also, as a rule, thick, though never quite as thick as the first one, but on the contrary higher than that. Concerning the interbranchial ridge 2 it should be mentioned that this, as we have seen, reaches so far dorso-medially as to meet the aortal ridge either about midway between the first interbranchial ridge and the carotid canal (text-fig. 36, pl. 51) or somewhat more backwards (pl. 44) and thus nearer to the carotid canal. The third branchial fossa (k_3, text-figs. 4, 12, 13, 33, 36, 39; section series C, nos. 111—124; section series F, nos. 33, 36—51; pls. 15, 22, 44, 51), which is bounded anteriorly by the interbranchial ridge and interbranchial septum 2 and posteriorly by the interbranchial ridge and interbranchial septum 3, is still bigger than the second one. The interbranchial septum 3 (ibs_3) is higher but narrower than the one next in front. And concerning the interbranchial ridge 3 (ibr_3) it should be noticed that its medial part — which, as has already been pointed out, continuous to the aortal ridge dorsomedially — is situated on the anterior portion of the orbital prominence, close behind the subnasal fossa (*f. sn*). The fourth branchial fossa (k_4, text-figs. 4, 11—13, 33, 36, 39, section series C, nos. 93—120; section series F, nos. 15—57; pls. 15, 22, 51), which is situated between the interbranchial septum and interbranchial ridge 3 anteriorly and the inter-



Text-fig. 34. *Cephalaspis hoeli.*

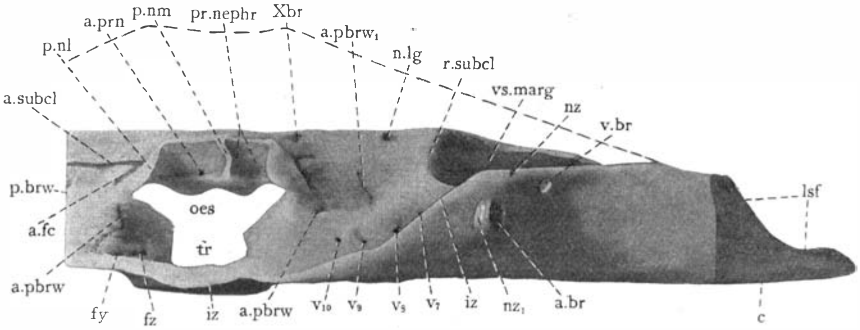
Text-fig. 34. *Cephalaspis hoeli.* Restoration of a posterior part of the cephalic shield in dorsal view. The most dorsal parts are missing. After a model in wax made from section series F. $^6/_1$.

a. eff. com, space which lodged the arteria branchialis efferens communis; *a. fc,* groove for an artery arisen by the confluence of the two most posterior efferent branchial arteries; *a. eff*$_7$—*a. eff*$_9$, canals for the efferent branchial arteries 7—9; *a. pbrw*, *a. pbrw*$_1$, canals for arteries to the posterior surface of the postbranchial wall; *a. subcl,* canal for the arteria subclavia; here not closed for a certain stretch; *c*, cornu; *fy*, canal brobably for a ventral superficial longitudinal vein; *fz,* fine canal probably for a vessel; *iz*, interzonal part of the shield; *n. lg*, canal probably for the n. lineae lateralis; *nz*, *nz*$_1$, canals probably for nerves to the pectoral fin; the canal *nz*$_1$ probably transmitted also a vein; *oes,* oesophageal division of the foramen for the oesophagus and the truncus arteriosus; *p. nl,* lamella of bone which protected the pronephros on the lateral side; *p. nm,* lamella of bone dividing the anterior part of the space for the pronephros; *p. brw*, postbranchial wall; *p. sh,* endoskeletal shoulder-girdle; *pr. nephr*, space for the pronephros; *ps*, pectoral sinus; *r. subcl.* subclavian ridge; *sel*$_3$—*sel*$_6$, canals for the four posterior nerves to the lateral electric field; *tr*, division for the truncus arteriosus of the common foramen for the oesophagus and the truncus arteriosus; *v. br*, canal probably for the vena brachialis; *vest*, vestibular division of the labyrinth cavity; *v. marg*, canal for the marginal vein; *vs. marg*, marginal vein sinus; *v*$_5$—*v*$_{10}$, canals for the ventral transversal superficial veins 5—10; X$_{\mathrm{br1}}$, canal for the first branchial branch of the n. vagus; X$_{\mathrm{br2}}$—X$_{\mathrm{br6}}$, two canals for the remaining posterior branchial branches of the n. vagus.

branchial septum and interbranchial ridge 4 posteriorly, is either of a similar size as the one in front or slightly smaller than that. The interbranchial septum 4 (*ibs*$_4$) is always narrower than the interbranchial septum 3, but approximately of a similar height as that. The dorsal, or more correctly the dorso-medial, part of the interbranchial ridge 4 (*ibr*$_4$) crossed the anterior portion of the otical prominence and continues, as we have found, to the aortal ridge. Whereas each one of the three anterior interbranchial ridges (*ibr*$_1$—*ibr*$_3$) as already mentioned, in certain forms appears to be provided with a groove in its longitudinal direction (*a. eff*$_1$—*a. eff*$_3$), a groove which leads to the anterior part of the aortal groove and which certainly was caused by an efferent branchial artery, the fourth as well as all the other interbranchial ridges following behind the fourth one never exhibit any grooves of this sort. The branchial fossae (*k*$_5$—*k*$_{10}$, text-figs. 4, 9—13, 33, 36, 39, 40; section series C, nos. 85—114; section series F, nos. 13—61; pls. 15, 22, 51) following behind the fourth one, as well as the interbranchial septa (*ibs*$_5$—*ibs*$_9$) and interbranchial ridges (*ibr*$_5$—*ibr*$_9$) separating them, diminish fairly gradually in size backwards so that the 10th branchial fossa is always very small. Moreover these posterior branchial fossae also change their shape somewhat backwards, so that the relative difference in width between their dorsal and middle thirds on the one hand and their ventral third on the other becomes less conspicuous and so that, as a whole, they appear narrower than the ones in front. In addition in certain forms, such as *C. hoeli*, they are as a whole relatively deeper than the four anterior ones. And finally it should be noticed that, in accordance with the curvature and forward inclination of the postbranchial wall, they may in several forms, such as *C. hoeli* (text-figs. 33, 39, 40), change their position from a transversal one to a more oblique one or to one almost parallel with the median longitudinal plane through the head. The four anterior ones, on the contrary, always occupy a position almost straight transversal in relation to the longitudinal axis of the animals. The interbranchial septa (ibs_5—ibs_9) situated between the five posterior branchial fossae are all rather thin and dicrease in height backwards. Of the posterior interbranchial ridges the fifth (ibr_5) continues dorso-medially across the most posterior part of the otical prominence and thus on the ventral surface of the endocranium, while the ones behind that (ibr_6—ibr_9) all pass dorso-medially wholly on the postbranchial wall, on which the sixth (ibr_6) seventh (ibr_7) and eight (ibr_8) ones may be traced as far dorso-medially as to the strong ridge *r. eff. com*, while the ninth (ibr_9) never reaches as far as that, but unites with the eighth already a considerable distance latero-ventrally to the ridge *r. eff. com.*

Of the branchial fossae the six anterior ones are situated on the internal surface of the lateral part of the visceral endoskeleton, while the remaining ones following behind the sixth one may be considered to lie on the anterior surface of the postbranchial wall. On this surface of the postbranchial wall we find otherwise most dorso-medially, above the foramen for the oesophagus or the oesophagus division of the common oesophagus-truncus arteriosus foramen, the strong ridge *r. eff. com*, which has already been referred to. This ridge (text-figs. 4, 9, 10, 33, 36, 39 40; section series F, nos. 1—28; pl. 46, fig. 1; pl. 47, fig. 1; pls. 51, 52, 58) lies in the straight posterior continuation of the aortal ridge beneath the aortal canal through the postbranchial wall. As it lodged in its interior a chamber that opens antero-dorsally into the most anterior part of the aortal canal — a chamber which, as we shall see, was occupied by an artery formed by the confluence of certain of the posterior efferent branchial arteries — it will be referred to as the ridge for the arteria branchialis efferens communis. In addition to this ridge we find, at least in *C. hoeli*, also on the anterior surface of the postbranchial wall a more or less distinct fossa close laterally to the ventral part of the truncus arteriosus foramen or its homologue and thus medially to the ventral part of the branchial fossa 10 (text-figs. 33, 39). It seems not quite impossible that this fossa may be a vestigal 11th branchial fossa; but it is fully clear that, if this is the case, it must have lost its gill, so that it had no respiratory function any more.

Finally attention should be called to the fact that, both on the internal surface of the lateral part of the visceral endoskeleton and on the anterior surface of the postbranchial wall, we find the openings of numerous canals.



Text-fig. 35. *Cephalaspis hoeli.* The right cornu, the right endoskeletal shoulder-girdle and a right part of the postbranchial wall in posterior view. Restoration made after section series F. $^{7}/_{1}$.

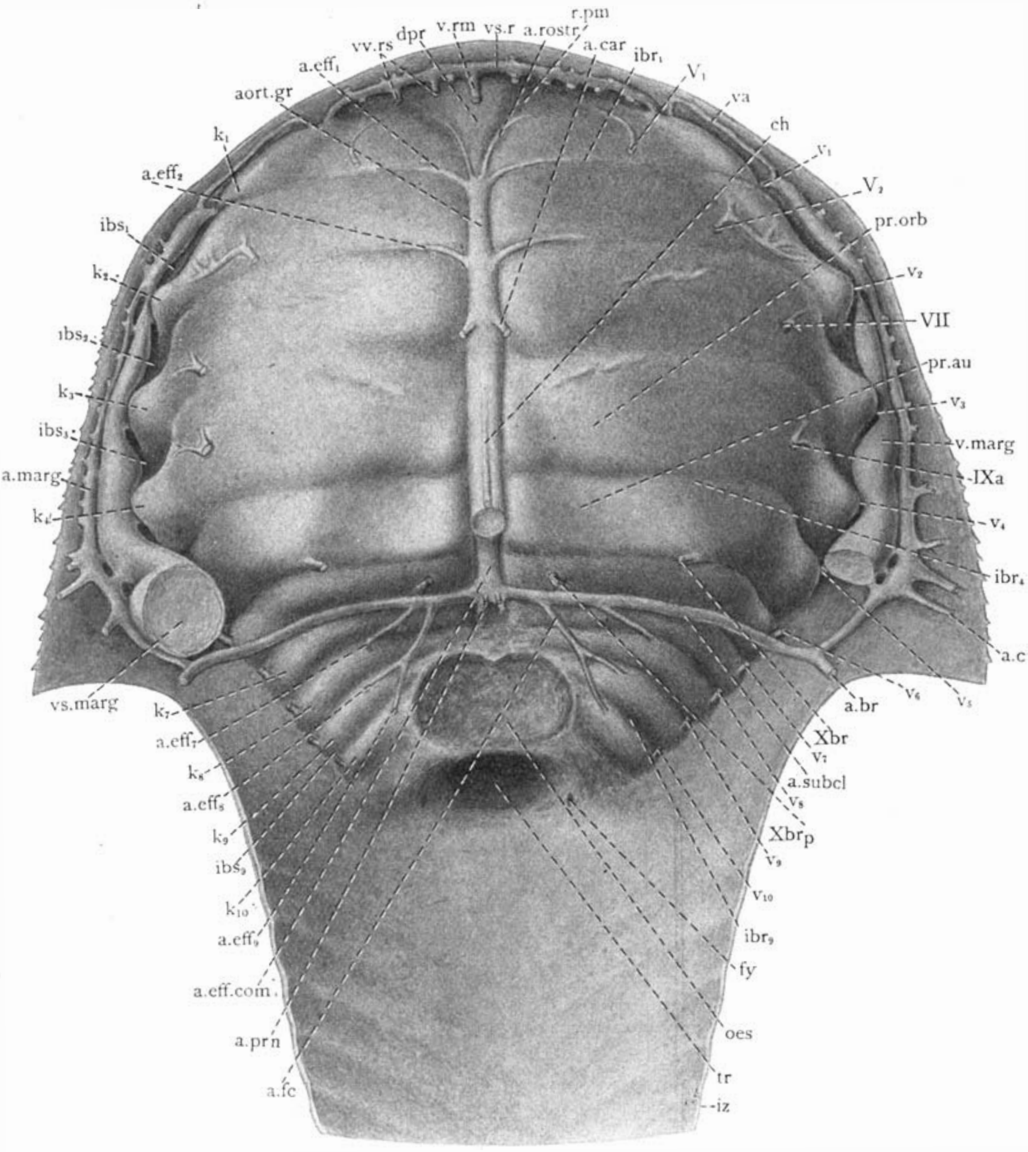
a. br, canal for the brachial artery; *a. fc,* groove for an artery arisen by the confluence of the two most posterior efferent branchial arteries; *a. prn,* canal probably for a small arterial branch to the pronephros; *a. pbrw*, *a. pbrw*$_1$, canals for arteries to the posterior surface of the postbranchial wall; *a. subcl,* canal for the arteria subclavia, here not closed for a certain stretch; *c,* cornu; *fy,* canal for a ventral superficial longitudinal vein; *fz,* fine canal probably for a vessel; *iz,* interzonal part of the shield; *lsf,* emargination indicating the position of the lateral electric field; *n. lg,* foramen perhaps for the n. lineae lateralis; *nz, nz*$_1$, canals probably for nerves to the pectoral fin; the last-mentioned one probably transmitted also a vein; *oes,* oesophageal division of the foramen for the oesophagus and truncus arteriosus; *p. brw,* postbranchial wall; *p. nl,* lamella of bone which protected the pronephros from the lateral side; *p. nm,* lamella of bone dividing the anterior part of the space for the pronephros; *pr. nephr,* space for the pronephros; *r. subcl,* subclavian ridge; *tr,* division for the truncus arteriosus of the common foramen for the oesophagus and truncus arteriosus; *v. br,* canal probably for the vena brachialis; *vs. marg,* marginal vein sinus; v_7—v_{10}, canals for the ventral transversal superficial veins 7—10; X$_{\text{br}}$, groove and foramen for the most posterior branchial trunk of the n. vagus.

As has already been pointed out, the n. profundus, after it had perforated the ethmoidal region, entered the visceral endoskeleton in front, i. e the rostral part of the visceral endoskeleton. More exactly, it pierced the lateral portion of that part of the visceral endoskeleton, within which its canal, V_1, could be well exposed in several specimens (text-figs. 4, 13, 23—25, 27, 28, 36; section series C, nos. 72—88; section series D, nos. 1—20; pl. 13 fig. 3; pls. 14, 15, 17, 18; pl. 19, fig. 1; pls. 20, 21, 27, 28, 29, 39, 44, 45, 49, 50; pl. 54, fig. 1; pls. 55, 57, 58). As is clearly seen, its canal is there always rather wide. And it is particularly interesting to find that at least in most forms — such as *Kiaeraspis*, *Boreaspis*, *Hoelaspis*, and many *Cephalaspis*-species (*C. hoeli*, *C. heintzi*, *C. spitsbergensis*, *C. arcticus*) — it does not open until very far forwards in the most antero-ventral part of the oralobranchial chamber, more exactly, close behind the antero-ventral part of the prebranchial ridge and, thus close to the anterior border of the first branchial fossa. During its passage through the rostral part of the visceral endoskeleton it gives off several branches particularly in the most anterior part. The majority of these branches terminate in the exoskeleton and must therefore certainly have transmitted general cutaneous nerve branches; but, as is seen from text-fig. 36 and pl. 51, it is also obvious that one of its most distal branches went to the dorsal side of the mouth. Hence this last-mentioned branch may perhaps, at least partly, have been composed of communis fibres. The most distal part of the profundus canal still retaining a rather considerable width, it is obvious that the part of the n. profundus that reached the first branchial fossa still was a strong nerve. Since, as we shall see, there is much reason to believe that in the anterior part of the first branchial fossa there was visceral musculature and since no other nerve than the n. profundus, seems to have reached as far forwards, it is very likely that the n. profundus besides its other components, also was composed of a viscero-motor component for the innervation of the said musculature.

The canal for the n. trigeminus proper (V_2, text-figs. 4, 13, 23—25, 27, 28, 36; section series C, nos. 81—91; pl. 14; pl. 19, fig. 1; pl. 21; pl. 23, fig. 3; pls. 28, 29, 45, 49—51; pl. 54, fig. 1; pls. 55, 57, 58), after it had left the orbito-temporal region, continued antero-latero-ventrally through the anterior portion of the lateral part of the visceral endoskeleton to the oralo-branchial chamber. In *Kiaeraspis* (text-figs. 4, 28, 36; pls. 49, 50, 51, 55, 57), *Hoelaspis* (pls. 44, 45), *Boreaspis* (pls. 14, 15) and certain *Cephalaspis*-species, as *C. arcticus* (pl. 28), it is very long and reaches the oralo-branchial chamber very far ventro-laterally, while in other forms, such as *Cephalaspis hoeli* (section-series C, nos. 81—91; pl. 21; pl. 23, fig. 3), it is considerably shorter, opening into the oralo-branchial chamber rather far dorso-medially. Among the forms belonging to the former of these two categories, it has at least in *Kiaeraspis* (text-figs. 4, 36; pl. 51), its opening into the oralo-branchial chamber in the lateral part of the branchial fossa 2, close dorso-medially to the interbranchial septum 1. Among the forms pertaining to the other category, for instance in *C. hoeli* (pl. 23, fig. 3), its orifice into the oralo-branchial chamber seems to have been situated approximately between the middle thirds of the second and third branchial fossae, but it is continued there in an antero-latero-ventral direction by a rather deep groove. As this groove in the living specimens certainly was bridged over by the periost lining the oralo-branchial chamber, the n. trigeminus proper obviously must have passed antero-ventrally a certain stretch between this periost and the visceral endoskeleton before it pierced the periost and definitely emerged into the oralo-branchial chamber. Accordingly the n. trigeminus proper probably entered the oralo-branchial chamber far laterally in the branchial fossa 2 also in those forms in which its canal through the viscaral endoskeleton is short.

During its passage through the visceral endoskeleton the canal for the trigeminus proper gives off branches which go outwards to the exoskeleton and which certainly lodged general cutaneous nerve branches and partly also lateralis nerves, as we shall understand from the account of the sensory canal system given below. In addition, in certain well-preserved specimens, such as that of *C. hoeli* shown in pl. 23, fig. 3 and that of *C. arcticus* shown in pl. 28, it is clearly seen that rather soon after its entrance into the visceral endoskelelon there issues from the canal for the trigeminus proper a rather strong branch in an antero-ventral and slightly medial direction, a branch which leads to the dorso-medial part of the oralo-branchial chamber. This branch, which is letered V_{2v} in the figures, has such a course and position that it can hardly be imagined to have transmitted any pretrematic ramus of the n. trigeminus proper, but instead a branch of this nerve for the innervaton of certain internal medial parts of the soft tissues of the oralo-branchial chamber. And accordingly there is much reason to believe that this nerve-branch consisted of communis fibres and was a serial homologue to the visceral branches of the glossopharyngeus and vagus in *Petromyzon* (cf. text-fig. 38 and JOHNSTON 1905, pl. 5). Since, as we shall find, a serial homologue to the canal branch V_{2v} in the Cephalaspids is given off also from the canals for the n. facialis, the n. glossopharyngeus and the first branchial branch of the n. vagus the opinion advanced here concerning the function of the canal-branch V_{2v} gains of course very much in probalility.

In *Kiaeraspis* (text-fig. 36; pl. 51) it is highly interesting to find that the canal for the n. trigeminus proper within the oralo-branchial chamber is continued by a groove which almost immediately bifurcates into an antero-ventral and a postero-ventral branch. The former of these branches goes in a direction towards the transition between the first interbranchial septum and the first interbranchial ridge, while the latter, which is the widest one, passes off towards the deepest part of the lateral third of the second branchial fossa, dividing into three terminal branches. From these conditions, of course, it is easy to conclude that the n. trigeminus proper, at its entrance into the branchial fossa 2, gave off an antero-ventral branch towards the anterior border of the interbranchial septum 1, but that the main part of it went downwards along the medial side and posterior border of the same interbranchial septum. As the antero-ventral branch, as far as can be judged, cannot have crossed the first branchial fossa to reach the anterior side of that, and as in addition it probably was a serial homologue of the correspondingly passing fibres of the nn. glossopharyngeus and facialis, it cannot have been a pretrematic branch, but seems to have consisted only of viscero-motor fibres. And everything thus seems to show that the n. trigeminus proper had no pretrematic branches. It is also, as we shall, find quite evident



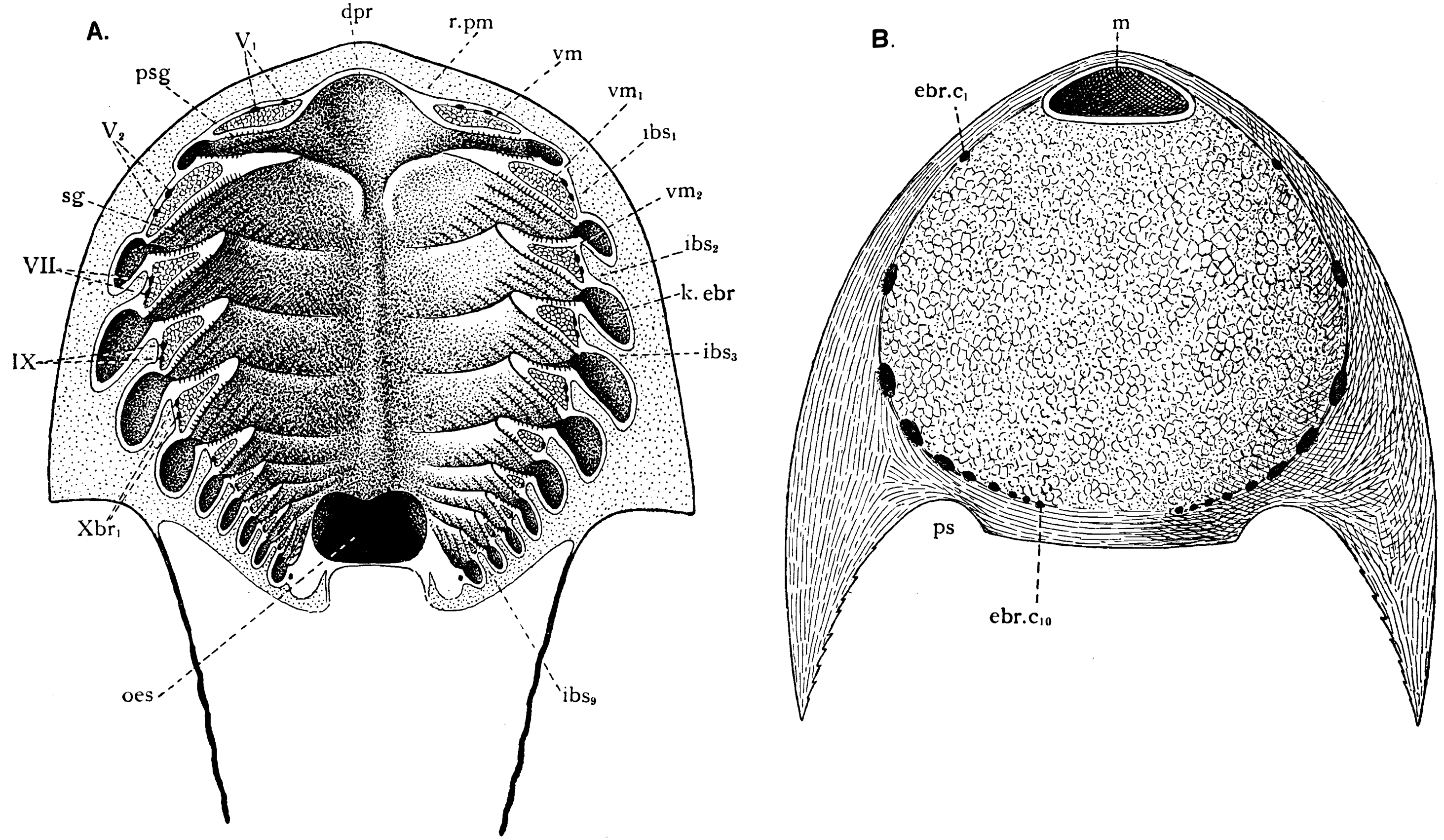
Text-fig. 36. *Kiaeraspis auchenaspidoides.*

Text-fig. 36. *Kiaeraspis auchenaspidoides*. Cast of the oralo-branchial chamber with certain posterior and lateral parts of the shield and certain canals. Dorsal viev. 8/1.

a. br, canal for the brachial artery; *a. c,* canal for the cornual artery; *a. car,* canal for the carotid artery; *a. eff*$_1$—*a. eff*$_2$, grooves for the first and second efferent branchial arteries; *a. eff*$_7$—*a. eff*$_{10}$, canals for the efferent branchial arteries 7—10; *a. eff. com,* canal for the arteria branchialis efferens communis; *a. fc,* groove for an artery arisen by the confluence of the two most posterior efferent branchial arteries; *a. marg,* canal for the marginal artery; *aort. gr,* aortal groove; *a. prn,* canal for an arterial branch to the pronephros; *a. rostr,* groove for the rostral artery (the premandibular efferent branchial artery); *a. subcl,* canal for the arteria subclavia; *ch,* canal for the notochord; *dpr,* area which formed the dorsal boundary of the mouth cavity; *fy,* canal for a ventral superficial longitudinal vein; *ibr*$_1$—*ibr*$_9$, interbranchial ridges; *ibs*$_1$—*ibs*$_9$, interbranchial septa; *k*$_1$—*k*$_{10}$, branchial fossae 1—10; *iz,* ventral portion of the interzonal part of the cephalic shield; *oes,* opening for the oesophagus; *pr. au,* impression of the otic prominence; *pr. orb,* impression of the orbital prominence; *r. pm,* prebranchial ridge; *tr,* opening for the truncus arteriosus; *v*$_1$—*v*$_{10}$, canals for the ventral transversal superficial veins; *va,* canal probably for an arterial branch from the truncus arteriosus; *v. marg,* canal for the marginal vein; *v. rm,* canal for the median rostral vein; *vs. r,* rostral vein sinus; *vs. marg,* marginal vein sinus; *vv. rs,* canals for the lateral rostral veins; V_1, canal for the n. profundus; V_2, canal for the trigeminus proper; VII, canal for the n. facialis; IX*a*, canal for the n. glossopharyngeus from the labyrinth cavity to the oralo-branchial chamber; X_{br}, X_{brp}, canals for the branchial branches of the n. vagus (behind the first one).

that the n. trigeminus proper in its mode of branching was only slightly more specialized than the branchial nerves situated behind it. And accordingly we find here conditions which to a certain degree remind us of those in *Petromyzon*, but which, however, are still more primitive than these. (Cf. JOHNSTON 1905).

The canal for the n. facialis (VII, text-figs. 4, 13, 23—25, 27, 28, 36; section series, C, nos. 87—105; pls. 17, 18, 20, 21; pl. 23, fig. 3; pl. 24, fig. 1; pls. 25—29, pls. 44, 45, 49—51, 54, 55, 57), which, as has already been explained, issues from the antero-dorso-lateral part of the vestibular division of the labyrinth cavity soon leaves the otic region, entering the lateral part of the visceral endoskeleton of its side. For a detailed study of it during its passage through the visceral endoskeleton we shall first turn to *Kiaeraspis*. In that form (text-figs. 4, 27, 28, 36; pls. 49—51, 54, 55, 57) it is very long, only opening into the oralo-branchial chamber in the lateral part of the branchial fossa 3 close dorso-medially to the interbranchial septum 2. It seems very likely that already soon after its entrance into the visceral endoskeleton it gave off a rather strong branch to the dorso-medial part of the oralo-branchial chamber, a branch which would have been a serial homologue to the branch V_{2v} and V_{1v} of the trigeminus and profundus canals and which, like this, would have given passage to a visceral nerve-branch. No quite certain decision is possible in this case, however, since the *Kiaeraspis*-specimens at disposal all are somewhat defective so far as the proximal part of the facialis canal is concerned. During its passage within the visceral endoskeleton the facialis canal further gives off branches to the external parts of the cephalic shield, branches which certainly were traversed by fine nerve-branches composed of general cutaneous fibres and lateralis fibres. Close to the distal end the facialis canal divides into an anterior branch which goes antero-latero-ventrally towards the anterior border of the interbranchial septum 2, and a posterior branch which turns postero-ventrally towards the posterior border of the same interbranchial septum. The latter branch soon breaks up into a number of fine ramuli, several of which rather soon take a superficial direction to the outer parts of the skeleton of the shield, a fact which shows that they must have transmitted general cutaneous nerve branches and which in addition seems to indicate that the entire big branch of the n. facialis that had its exit through the posterior branch of the facialis canal was composed solely of general cutaneous fibres. And as this seems to be so, it follows that the nerve-branch of the n. facialis that emerged through the anterior branch of the canal must, of course, have consisted of the viscero-motor fibres for the visceral musculature, and accordingly it cannot have been a pretrematic branch, since the pretrematic branches, as a rule, are composed only of communis fibres. In *Hoelaspis* (pls. 44, 45) the facialis canal (VII) has a similar length as in *Kiaeraspis*. But I cannot find that it bifurcates in its most distal part as in that form. On the other hand, it is fully obvious that in *Hoelaspis* it had a branch (VII_v) for a visceral nerve-branch. Finally in the *Cephalaspis*-species (section series C, nos. 87—105; pls. 17, 18, 20, 21; pl. 23, fig. 3, pls. 24—29) the facialis canal (VII) is generally considerably shorter than in *Kiaeraspis* and *Hoelaspis*, its opening into the oralo-branchial chamber being situated much more dorso-medially than in these. But as it is continued antero-ventro-laterally by a deep groove, which certainly — at least most proximally — was bridged over by the periost, it is very probable that the n. facialis quite as the n. trigeminus proper in them arrived into the oralo-branchial chamber only a certain distance antero-latero-ventrally to the opening of its canal, and thus that the conditions with regard to this nerve were not essentially different from those in *Kiaeraspis* and *Hoelaspis*. In the specimen of *Cephalaspis hoeli* figured in pl. 23, fig. 3, it is distinctly seen that a rather thick branch (VII_v) is given off from the facialis canal to the dorso-medial part of the oralo-branchial chamber; and from its course and position it is easy to conclude that this branch must be a serial homologue of the branches V_{1v} and V_{2v} of the canals for the n. profundus and the n. trigeminus proper respectively, and that, therefore, it probably transmitted the r. visceralis of the n. facialis. In the specimen of *C. heintzi* shown in pl. 29 the facialis canal has a rather strong posterior branch which quite distinctly leads to the exoskeleton and which gave passage either to a nerve-branch of general cutaneous fibres or of lateralis fibres or of both these sorts of fibres.



Text-fig. 37. Two attempted restorations.

A. Horisontal section through the ventral part of the head of *Kiaeraspis* showing the assumed position of the gill-sacs etc.

B. Cephalic shield of a *Cephalaspis* in ventral view with the external branchial openings.

dpr, area which formed the roof of the mouth cavity; *ebr.* c_1, *ebr.* c_{10}, external branchial openings; ibs_1, ibs_2, ibs_3, ibs_9, interbranchial septa; *k. ebr*, external duct of the gill sac 3; *m*, mouth opening; *oes*, oesophagus; *ps*, pectoral sinus; *psg*, prespiracular gill sac *r. pm*, prebranchial ridge; *sg*, spiracular gill sac; *vm*, vm_1, visceral muscles of the gill sacs; V_1, n. profundus; V_2, branches of the n. trigeminus proper; VII, branches of the n. facialis; IX, branches of the n. glossopharyngeus; X_{br_1}, branches of the vagus (supposed position).

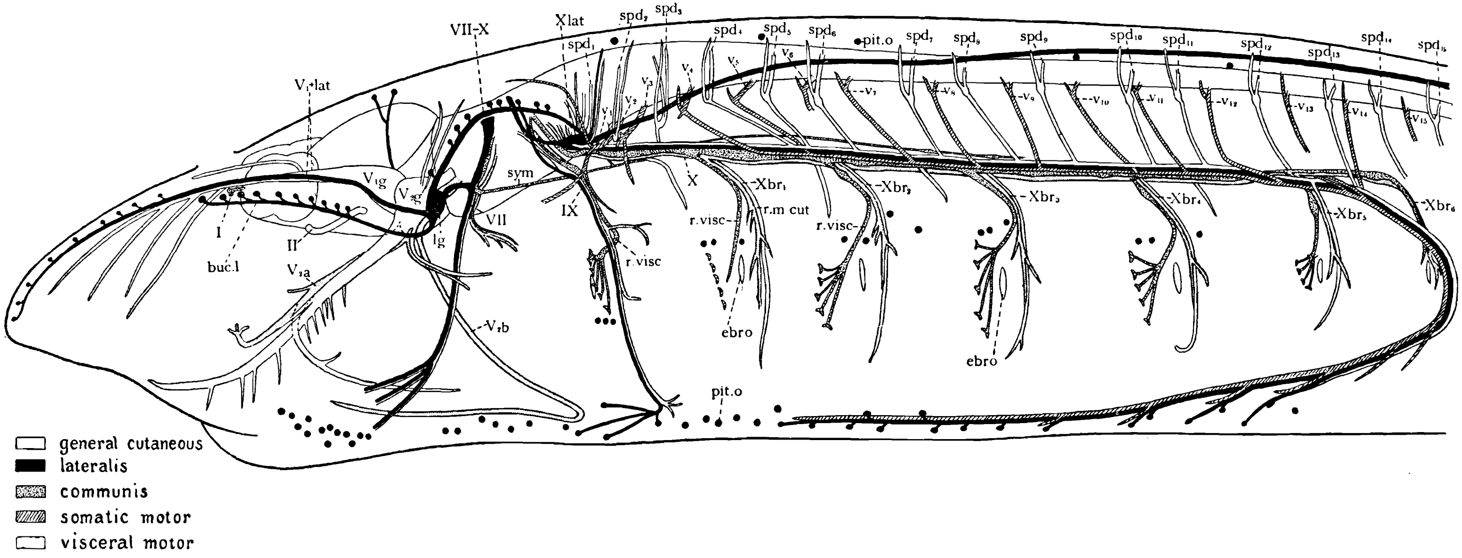
From this account of the facialis canal we are thus able to conclude that the n. facialis consisted not only of communis, viscero-motor and lateralis fibres, but that probably, quite as in the Petromyzontids, it also had a general cutaneous component (cf. text-figs. 38, 42 in the present work; cf. also JOHNSTON 1905, p. 198; HOLMGREN 1919, text-fig. 27, p. 88). In addition it is also very remarkable that it seems to have been without a pretrematic branch.

The n. glossopharyngeus, after traversing the postero-dorso-lateral part of the vestibular division of the labyrinth cavity, entered, as we have seen, the canal lettered IX *a* in the figures (text-figs. 4, 13, 23—25, 28, 36; section series C, nos. 97—109; pls. 20, 28—30, 44, 49—51, 54, 57; pl. 62, fig. 1). This canal, as has also been pointed out, soon leaves the otic region, continuing through the lateral part of the visceral endoskeleton of its side in an antero-ventro-lateral direction to the oralo-branchial chamber. In *Kiaeraspis* it is very long, opening into the lateral part of the branchial fossa 4, close dorso-medially to the interbranchial septum 3 (text-figs. 4, 28, 36; pls. 49—51, 54, 57). And it is also very noticeable that in this form it bifurcates, just before it reaches the branchial fossa 4, into an antero-ventro-lateral and a postero-ventro-lateral branch, both of which are rather short. More exactly, the former of these branches goes towards the anterior border of the interbranchial septum 3, while the latter takes its course towards the posterior border of the same interbranchial septum and breaks up into a number of fine branches, most of which enter the external parts of the cephalic shield, a fact which shows that they must have lodged general cutaneous nerve-branches. Accordingly we find that in *Kiaeraspis* the n. glossopharyngeus just at its entrance into the oralo-branchial chamber branched exactly as the n. facialis into an anterior branch, which must have consisted of viscero-motor fibres and have passed downwards along the anterior border of the interbranchial septum 3, and into a posterior branch, which was composed of general cutaneous fibres and which went downwards along the posterior border of the interbranchial septum 3. Whether the canal IX *a* in *Kiaeraspis* had a branch for a visceral nerve-branch cannot be decided with certainty. In *Hoelaspis* (pl. 44) and in the *Cephalaspis*-species known so far in detail (text-figs. 23—25, 46; section series C, nos. 97—109; pls. 20, 28—30; pl. 62, fig. 1) the canal IX *a* is much shorter than in *Kiaeraspis*, opening into the oralo-branchial chamber much farther postero-dorso-medially than in that form. But at least in the *Cephalaspis*-species it is continued by a groove rather far in an antero-ventro-lateral direction, so that the n. glossopharyngeus, quite like the n. facialis and the n. trigeminus proper, in them probably in reality emerged into the oralo-branchial chamber almost at a corresponding place as in *Kiaeraspis*. Not infrequently the canal IX *a* in the *Cephalaspis*-species is strikingly wide (text-figs. 23—25, 46; pls. 28—30; pl. 62, fig. 1); and in the only case in which it could be studied in detail from the ventral side — in a specimen of *C. arcticus* (pl. 28) — it was found to give off a rather wide branch (IX_{av}) to the dorso-medial part of the oralo-branchial chamber, a branch which, as comparisons with recent forms suggest, can have been traversed only by a nerve-branch consisting of communis fibres — that is to say a nerve-branch homologous with the r. visceralis of the corresponding nerve in *Petromyzon* (cf. text-fig. 38).

From the conditions of its canal we are evidently justified in concluding that the n. glossopharyngeus consisted of communis fibres, general cutaneous fibres and viscero-motor fibres. As we shall find from the disposition of the sensory canal system, it is very likely that, in addition to the components enumerated, it also had a lateralis component.

The canal for the first branchial branch of the n. vagus (X_{br_1}, text-figs. 4, 13, 28, 33, 34, 36; section series A, nos. 62—65; section series C, nos. 79—86; section series E, nos. 7—11; section series F, nos. 2—3; pls. 28, 52, 57) lies, as we have seen, entirely in the ventral wall of the otic region, and never extends into the visceral endoskeleton. In *Kiaeraspis*, as has also been mentioned above (p. 68), it is clearly seen that it gives off a rather strong branch (X_{br_1v}, pl. 52) in a postero-ventral direction, a branch which leads to the oralo-branchial chamber, and which, on account of its position, seems to be a serial homologue to the branches V_{1v}, $V_{2\,v}$, VII_v, IX_{av}, from the canals for branchial nerves in front. And there is thus strong reason to believe that this branch gave passage to the visceral ramus of the first branchial nerve of the n. vagus. It is highly probable that the first branchial nerve of the n. vagus, after its entrance into the oralo-branchial chamber, passed ventrally in a similar way as the branchial nerves in front, and that its branches went close medially to or in the vicinity of the medial parts of the fourth interbranchial septum.

The canals for the 5 posterior branchial nerves of the n. vagus (X_{br_2}—X_{br_6}, X_{brp}, X_{br}, text-figs. 4, 13, 14, 33, 34—36, 39, 40; section series B, nos. 8—13; section series C, nos. 77—80; section series E, nos. 7—10; section series F, nos. 2—6; pl. 51) all pierce the dorso-medial part of the postbranchial wall, and are usually rather short, leading only to the postero-dorso-medial part of the oralo-branchial chamber. Their number seems to vary somewhat, but is probably generally 2 or 3. As far as can be judged from their canals, the posterior 5 branchial nerves of the n. vagus were associated with each other into two or three trunks when they perforated the postbranchial wall. Well within the oralo-branchial chamber, they must during their passage downwards soon have separated from each other. And though in the fossils there are no grooves for them in the oralo-branchial chamber, there is no



Text-fig. 38. *Petromyzon.* The cranial nerves and their components after JOHNSTON 1905.

ebro ,external branchial opening; *lg*, lateralis ganglion behind the trigeminus ganglion proper; *pit. o*, organs of the lateral line system; *r. m cut*, rami musculo-cutanei of the n. glossopharyngeus and of the n. vagus; *r. visc*, rami viscerales of the n. glossopharyngeus and of the n. vagus; spd_1--spd_{15}, dorsal spinal nerve-roots; *sym*, symphathetic trunk and ganglia; v_1--v_{15}, ventral spinal nerve roots; I, n. olfactorius; II, n. opticus; $V_1 + lat$, n. profundus, accompanied by lateralis fibres; V_1g, profundus ganglion; V_2, trigeminus proper; V_2g, trigeminus ganglion proper; V_2a, V_2b, branches of the n. trigeminus proper, generally referred to in the literature as the ramus maxillaris and the ramus mandibularis respectively; VII, n. facialis; VII—X, trunk of lateralis fibres connecting the lateralis ganglion *lg* and X_{lat}; IX, n. glossopharyngeus; X, n. vagus; X_{br1}—X_{br6}, the branchial branches of the n. vagus; X_{lat}, lateralis ganglion associated with the vagus ganglia.

reason to suspect that, with regard to their relations to the branchial fossae, interbranchial septa and interbranchial ridges, they were essentially different from the branchial nerves in front.

Concerning the n. vagus, we have thus been able to establish that its roots emerged from the endocranium and had its ganglionic complex postero-dorsally to the postbranchial wall, and that its five posterior branchial nerves, obviously more or less closely associated with each other to a truncus epibranchialis, also for a short distance had their course postero-dorsally to the postbranchial wall. Further it should be noticed that there is every reason to believe that the n. vagus was composed not only of communis and viscero-motor fibres, but that it also had general cutaneous and lateralis components.

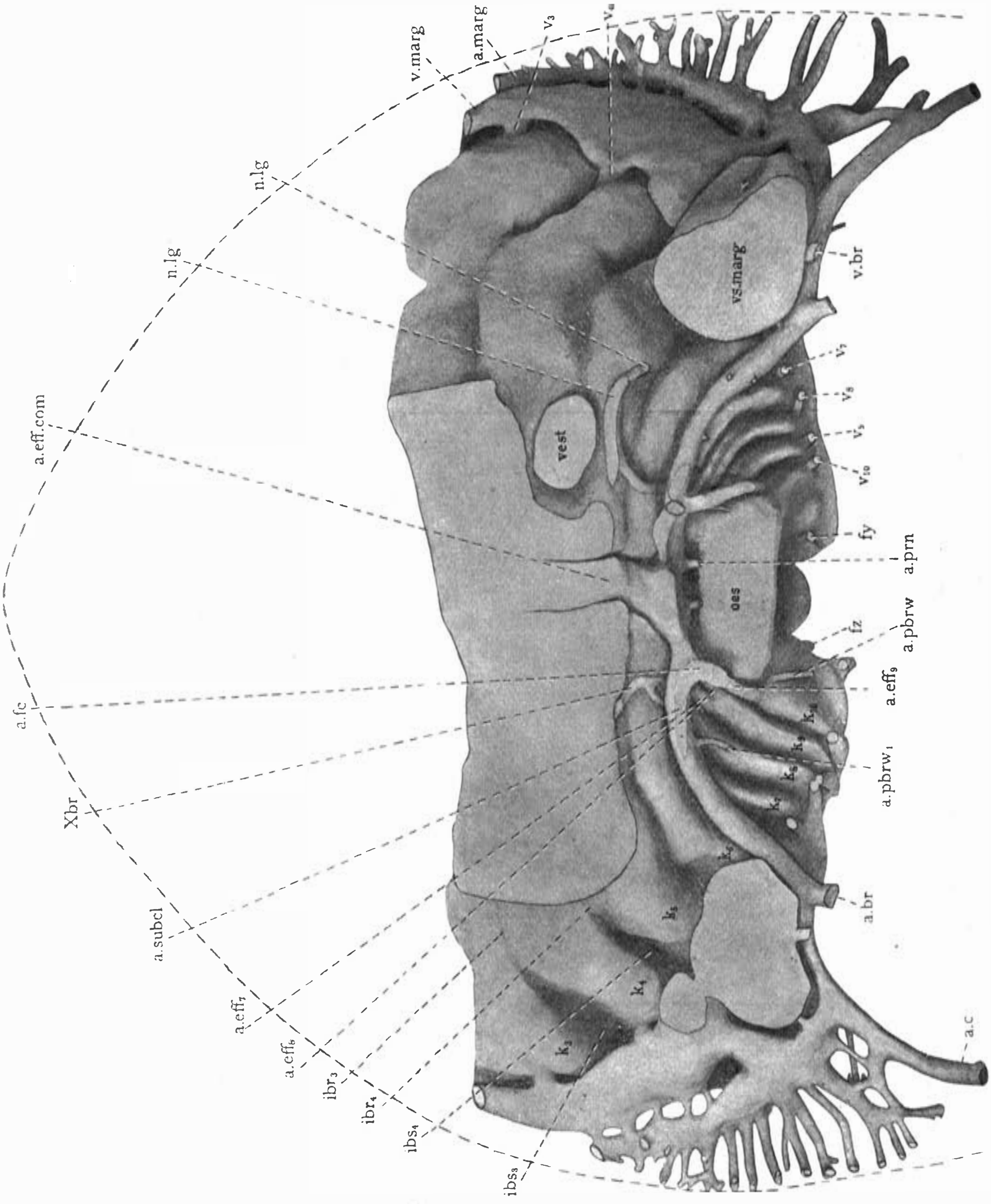
According to the knowledge we now possess of their canals, we are thus able to conclude the following concerning the branchial nerves. 1) The n. profundus was presumably developed exactly as the typical branchial nerves, and, like them, had a viscero-motor component. It thus seems to have retained more primitive conditions than in any other craniate vertebrate known so far. 2) With regard to its mode of branching the n. trigeminus proper was evidently less specialized and more like the branchial nerves behind it than in any craniate vertebrate in which it is known otherwise. But it is worthy of notice that, as a whole, it seems to have been more in accord with the corresponding nerve of the Petromyzontids than with that of any other form. 3) The n. facialis obviously had a general cutaneous component — a condition which otherwise, as far as is known, is the case only in Petromyzontids (cf. JOHNSTON 1905, pp. 185, 198). 4) The n. glossopharyngeus and the n. vagus both had general cutaneous components, and both of them passed a certain stretch postero-dorsally to the postbranchial wall before they reached the oralo-branchial chamber. 6) All the branchial nerves were without pretrematic branches, but had in addition a strong visceral branch. And we thus find that in these respects they were exactly like those in Petromyzontids (cf. JOHNSTON 1905, pp. 169—176). 7) All the branchial nerves went down to the ventrolateral parts of the branchial fossae and, except the n. profundus, they continued from there farther ventrally along the medial side of, or at least chiefly medially to, the interbranchial septa — in any case, however, medially to the visceral endoskeleton. The n. profundus, on the other hand, passed downwards in the anterior part of the first branchial fossa, slightly posteriorly to the antero-ventral part of the prebranchial ridge, but it too had its course internally to the visceral endoskeleton.

While, as is well known, the branchial nerves in fishes pass downwards along the postero-lateral side of the branchial arches, entirely outside the branchial skeleton, they enter in the Petromyzontids rather soon during their course downwards the branchial basket, continuing within this downwards chiefly medially to the branchial bars (cf. Sewertzov, 1916, pp. 12—79; 1917, pp. 495—510; Goette 1901, pp. 535—548, 562—574, Moroff 1902; Jacobshagen 1920, pp. 111—116). Now it is not difficult to see that, with regard to the relations between the branchial nerves and the visceral endoskeleton, the Cephalaspids were not in accord with the fishes but that in this respect they very distinctly pertained to the *Petromyzon*-type. And as in addition the branchial nerves of the Cephalaspids passed almost exactly in such a way in relation to the interbranchial septa and ridges as the branchial nerves of the Petromyzontids do in relation to the branchial arches, it is beyond question that the posterior interbranchial septa and ridges of the Cephalaspids, correspond to and are exact homologues of approximately the dorsal halves of the branchial arches of the Petromyzontids. More exactly, it is the seven most posterior interbranchial septa and ridges of the Cephalaspids — that is to say, the interbranchial septa and ridges 3—9 — that, since they were related to the glossopharyngeus and vagus nerves, correspond to the dorsal halves of the seven branchial arches in the Petromyzontids. On the other hand, it is not easy to find any exact homologues in the adult Petromyzontids to the interbranchial septa and ridges 1 and 2 of the Cephalaspids; but as we shall find from the account given below of the Petromyzontids, such homologues are nevertheless present, though they are distinctly seen only in the larvae. The interbranchial septa and ridges 1 and 2 of the Cephalaspids, as being the undoubted serial homologeus to the interbranchial septa and ridges behind and thus also to the branchial arches of the Petromyzontids, must, however, on account of their relations to the nerves, quite certainly represent the dorsal halves of the mandibular and hyoid arches respectively. In this connection attention should also be called to the fact that in the Cephalaspids the prebranchial ridge, on account of its relation to the n. profundus and its position in front of the first branchial fossa, seems so be a serial homologue of the interbranchial ridges and septa. And if this is true, it must of course represent the dorsal half of the premandibular arch, an opinion which, as we shall find, is supported by what will be set forth below regarding the efferent branchial arteries.

From what has now been advanced concerning the homologues of the interbranchial septa and ridges as well as of the prebranchial ridge, it follows that of the three first branchial fossae the first one occupied a prespiracular, the second one a spiracular and the third one a hyoidean position. And we thus find that the Cephalaspids had functional gills farther forwards than other craniate vertebrates in which the conditions with regard to the respiratory apparatus are known in detail. In the Cephalaspids in fact, there were two anterior gills and two anterior external branchial openings more than in the Petromyzontids and one anterior gill and one anterior external branchial opening more than in those fishes in which there is a spiracular gill. Accordingly we find in the Cephalaspids with regard both to the degree of development of the visceral endoskeleton and to the presence of anterior gills more primitive conditions than in fishes and recent Cyclostomes. And from these conditions it is at once obvious that the Cephalaspids cannot have had the anterior parts of the visceral skeleton transformed into jaws but must have been agnathous forms and, what is still more important, even primitively agnathous forms.

In the general description given of the oralo-branchial chamber (p. 46 above) it was pointed out that the gills of the Cephalaspids could not have been like ordinary fish-gills but must have been more or less sac-like as in Cyclostomes. And from what has been brought forward here concerning the branchial fossae and interbranchial septa and ridges, it now is still more obvious that this really was the case. In the subsequent account, therefore, the gills will be referred to as gill-sacs. And accordingly there was one prespiracular gill-sac, one spiracular gill-sac, one hyoid gill-sac, one glossopharyngeal gill-sac and six gill-sacs that were supplied by the n. vagus (text-fig. 37 A). Since the branchial nerves all seem to have been without a pretrematic branch each one of them went posterior to its gill-sac exactly as in the Petromyzontids.

If a velum was present in the Cephalaspids it must have been a medially produced part of the wall of soft tissue that from the interbranchial septum and ridge 1 projected into the oralo-branchial chamber between the prespiracular and spiracular gill sacs (text-fig. 37 A). In any case it is thus obvious that the prespiracular gill-sac was situated either in front of the velum itself or of a portion of tissue that could have given rise to a velum. And it is thus quite certain that it must have corresponded to the invagination of the *Petromyzon*-larva that always occurs on each lateral side of the mouth cavity just in front of the velum (*p. sh*, text-fig. 97 B, C), although this invagination never develops into a gill-sac and never opens outwards. As now in the *Petromyzon*-larva the stomodaeum invagination reaches as far back as the velum and has such on extension that the anterior surface of the velum as well as the entire mouth cavity is lined by ectoderm (text-figs. 89, 96), the invagination on the lateral side of the mouth cavity just in front of the velum is evidently also lined by the ectoderm. And as this is the case, there is much reason to believe that the prespiracular gill-sac of the Cephalaspids too was formed by the ectoderm of the stomodaeum invagination. On account of their position behind the velum or the homologue of that and, as we shall find, also on account of their position deep inwards the spiracular gill-sac, as well as all the



Text-fig. 39. *Cephalaspis hoeli.*

Text-fig. 39. *Cephalaspis hoeli.* Cast of the posterior half of the oralo-branchial chamber with the canals in the postbranchial wall and the postero-lateral parts of the shield. The most dorsal parts have been removed down to the level of the canal for the arteria branchialis efferens communis. Restoration made after section series F. 7/1.

a. br, canal for the arteria brachialis; *a. c*, canal for the arteria cornualis; *a. eff. com*, canal for the arteria branchialis efferens communis; $a.\,eff_7$—$a.\,eff_9$, canals for the three most posterior efferent branchial arteries; *a. fc*, canal for an artery arisen by the confluence of the two most posterior efferent branchial arteries; *a. marg*, canal for the arteria marginalis; *a. pbrw*, $a.pbrw_1$, canals for arteries to the posterior surface of the postbranchial wall; *a. prn*, canal for an artery to the pronephros; *a. subcl*, canal for the arteria subclavia; *fy*, canal probably for a ventral superficial longitudinal vein; *fz*, fine canal probably for a vessel; ibr_3—ibr_4, interbranchial ridges 3 and 4; here represented only by grooves; ibs_3—ibs_4, interbranchial septa 3 and 4 (represented by grooves); k_3—k_{10}, branchial fossae 3—10; *n. lg*, canal and groove probably for the n. lineae lateralis; *oes*, foramen for the oesophagus; *v. marg*, canal for the marginal vein; *vest*, vestibular division of the labyrinth cavity; *vs. marg*, marginal vein sinus; v_3—v_4, v_7—v_{10}, canals for the ventral transversal superficial veins 3, 4, 7—10; *v. br*, canal probably for the vena brachialis; X_{br}, canal for the most posterior branchial branches of the n. vagus.

gill-sacs posteriorly to that, in the Cephalaspids may very well be imagined to be of an entodermal origin. And if this is true, as it seems to be, the Cephalaspids would evidently also in this respect have been like the Cyclostomes, in which the post-velar gills, as well as the hyoid invagination, all are said to arise ontogenetically from the entoderm (cf. SEWERTZOV 1917, pp. 532—545; GOETTE 1901, pp. 535—548; MOROFF 1902; JAKOBSHAGEN 1920, pp. 111—116). In fishes, on the contrary, all the gills, as is well known, develop quite certainly from the ectoderm.

Above we have been able to establish that the interbranchial septa and ridges of the Cephalaspids are homologous to the dorsal halves of visceral arches of the Petromyzontids. And moreover it has been shown above that the interbranchial septum and ridges of the Cephalaspids had similar relations to the branchial nerves as the visceral arches of the Petromyzontids. To judge from these conditions, it seems very likely that the gill-sacs of the Cephalaspids had also similar positions in relation to the interbranchial septa and ridges as the gill-sacs of the Petromyzontids to the branchial arches. And if this conclusion is true, the gill-sacs of the Cephalaspids would obviously have been situated medially to the interbranchial septa and ridges in the dorsal and middle thirds of the branchial fossae, whereas the ventral thirds of these fossae would have been occupied solely by the external branchial ducts, which thus probably were rather long and directed rather obliquely postero-medio-ventrally. Besides their parts falling in the branchial fossae, however, the gill-sacs of the Cephalaspids must have had an additional ventral part which was curved much in a medial direction and which was situated in the dorsal (internal) parts of the soft tissue that closed the oralo-branchial fenestra and thus entirely ventro-medially to the branchial fossae. As far can be judged, the gill sacs of the Cephalaspids thus had a fairly considerable dorso-ventral extension and they were therefore certainly not spheroid-shaped as in Myxinoids, but probably, on the whole, as in the *Petromyzon*-larva (cf. text-fig. 37 A). It should also be added here that there is no reason to believe that there was a subeosophageal tube, as in the adult Petromyzontids, but that the gill-sacs probably opened inwards directly into the pharynx.

How I imagine the gill sacs of the Cephalaspids to have been situated is elucidated by text-fig. 37 A. The interbranchial ridges and septa formed, as we see from this text-figure, the most external parts of the walls between the different gill-sacs. Further inwards in each such wall, which we may call interbranchial wall, there followed the branchial nerve with its different branches and medially to that the visceral musculature. Concerning the visceral musculature it is worthy of remark that this certainly was very slightly specialized and that it was situated entirely medially to the visceral endoskeleton. In front of the prespiracular gill-sac it was probably situated chiefly close postero-medially to the prebranchial ridge, but a certain portion of it most forwards may perhaps have changed its function and been transformed into an oral musculature.

As far as can be judged from its branchial fossae, the prespiracular gill-sac was fairly big. And that — in connection with the circumstance that in the rostral artery, as we shall find, we presumably were concerned with the persisting rather well developed premandibular efferent branchial artery — renders it very likely that it was complete, i. e. that it was gill-bearing also on its anterior side. The tenth gill-sac, on the contrary, as it was very small and as it, as we shall find, had no efferent branchial artery from its posterior half, was probably gill-bearing only in its anterior half.

Like the gill-sacs, the external branchial openings were certainly generally 10 in number. They were situated postero-ventro-laterally to their respective gill-sacs on the ventral side of the head, more exactly close to and along the medial border of the ventral rim. Their approximate position is shown by the restorations given in text-figs. 37 B and 79 B.

From the account given of the gill-sacs it is fully obvious that the mouth must have been rather small and limited only to the most antero-medial portion of the oralo-branchial chamber situated anteriorly to the prebranchial ridge beneath the area *dpr*. The mouth-opening must therefore have had its position somewhat in the way shown in text-figs. 37 B and 79 B.

The circumstance that the gill-sacs were all situated beneath the endocranium and were present as far forwards as immediately behind the mouth-opening seems to indicate with a high degree of probability that there was no rasping tongue like that of the adult Petromyzontids and Myxinoids, but that the conditions in this respect probably were as in the *Petromyzon*-larva.

Finally attention should be called here to the fact that the conditions in the Cephalaspids with regard to the position of the external branchial openings and the mouth must have been exactly as in *Tremataspis* (text-fig. 83).

From what has been set forth concerning their visceral endoskeleton, their branchial nerves and their gill-sacs it is easely seen that the Cephalaspids, though in certain respects much more primitive than other craniate vertebrates known so far in detail, on the whole show very striking agreements with the Cyclostomes, particularly with the Petromyzontids.

After having briefly dealt with the homologues of the different parts of the visceral endoskeleton we shall again turn to its canals, beginning with those for the nerves to the lateral electric field.

As we have seen, five canals (sel_3—sel_6, and $sel_{1,2}$) for nerves to the lateral electric field leave the lateral and antero-lateral parts of the vestibular division of the labyrinth cavity. The four posterior ones of these canals — those which are lettered sel_3—sel_6 in the figures (text-figs. 9—12, 18, 19, 23—28, 34; section series A, nos. 50—109; section series C, nos. 76—124; pls. 14, 15; pls. 17, 18, 20—22, 24—31, 42, 44, 45; pl. 47, fig. 1; pls. 49, 50; pl. 54, fig. 1; pls. 55, 57, 58) — go in all forms, independently of and slightly diverging from each other, from the vestibular division of the labyrinth cavity to the lateral electric field. At their origin from the vestibular division they are all four of them situated rather deep in the otic region, but distally they gradually rise to the external surface of the visceral endoskeleton, so that finally they become situated immediately below the exoskeleton. At or just before entering the lateral electric field, they begin to branch; and within that field, at the bottom of which they finally arive, their branching is very abundant (pl. 29; pl. 30; pl. 31, fig. 3; pls. 49, 50). The most posterior one, sel_6, which is generally the thickest one of them, always has a somewhat backward course. The second one from behind, sel_5, usually goes, somewhat backwards too, though less than the former; but in certain cases it may pass almost straight laterally. The next one forwards, sel_4, may go either only very slightly backwards or straight laterally or else slightly forwards, while the fourth one from behind, sel_3, always turns off rather much forwards.

The most anterior one of the nerve-canals to the lateral electric field that leaves the vestibular division of the labyrinth cavity is, as we have seen, the one lettered $sel_{1,2}$ in the figures. This canal, which is very thick, goes, as we also have found, in all forms forwards laterally (ventro-laterally) to the orbit. In the *Cephalaspis*-species it regularly divides, as has already been mentioned (pp. 83—84), just anteoriorly or antero-laterally to the orbit, into two main branches *sel*$_1$ and *sel*$_2$ which, diverging slightly from each other, pass in an antero-latero-ventral direction to the anterior parts of the lateral electric field. Both these branches, which are thick and strong, are obviously serially homologous to the canals *sel*$_3$—*sel*$_6$, and, like these, they are distally situated very superficially and branch very abundantly on the bottom of the lateral electric field. Accordingly it is quite clear that the canal *sel*$_{1,2}$ of the *Cephalaspis*-species lodged the two most anterior nerves to the lateral electric field, and that the total number of nerves to this field of the *Cephalaspis*-species was six (pls. 17, 18, 20, 21, 24—30 etc.).

While the true *Cephalaspis*-species are thus characterized by the branching of the canal *sel*$_{1,2}$ close in front of or just antero-ventro-laterally to the orbit, we find in *Benneviaspis* (pl. 42, fig. 2) that this canal continued unbranched much farther forwards, and that it, anteriorly to the orbit, must have curved rather much laterally. In *Benneviaspis*, in fact, it does not divide into its two main branches — the canals *sel*$_1$ and *sel*$_2$ — until approximately midway between the orbital entrance and the lateral electric field. In *Hoelaspis* (pl. 45) the conditions with regard to the canal *sel*$_{1,2}$ are very similar to those in *Benneviaspis*; but the two main branches *sel*$_1$ and *sel*$_2$ there appear as independent canals perhaps still somewhat more distally, that is to say perhaps somewhat nearer to the lateral electric field than to the orbit. Finally in *Kiaeraspis* (text-fig. 28; pls. 49, 50, 55, 57, 58) and *Boreaspis* (pls. 14, 15) the branching of the canal *sel*$_{1,2}$ into the main branches *sel*$_1$ and *sel*$_2$ takes place only so close to the lateral electric field that, if we did not known the intermediary conditions in *Benneviaspis* and *Hoelaspis*, we should have been led to suspect that one of the six nerve-canals of the *Cephalaspis*-species — more exactly defined the second one from in front — had become reduced.

From the description now given of their canals we thus find that the lateral electric field of the Cephalaspids was supplied by six thick nerves, the anterior two of which went closely associated with each other in the same canal until just in front of the orbital entrance, or, in several forms, still further, even as far as until immediately before their entrance into the lateral electric field.

The canals for the nerves to the lateral electric field on the whole all run more superficially than the canals for the branchial nerves. Of these the canal for the n. profundus (V$_1$) always goes somewhat in front of and almost parallel with the canal *sel*$_1$ (*Cephalaspis*, text-figs. 23—25, 46, 47; section series A, nos. 122—155; section series C, nos. 72—94; pls. 17, 18, 20, 21; pl. 23, fig. 3; pls. 27—29; pl. 39), or the canal *sel*$_1$ and *sel*$_{1,2}$ in those cases when the latter canal does not divide into the canals *sel*$_1$ and *sel*$_2$ immediately anteriorly to the orbit (*Benneviaspis*, pl. 42; *Hoelaspis*, pl. 45; *Kiaeraspis*, text-figs. 27, 28; pls. 49, 50, 55, 57, 58). In all Cephalaspids the canal for the trigeminus proper (V_2) crosses the canal $sel_{1,2}$, on the ventral side (text-figs. 24, 28, 46, 47; section series A, nos. 112—155; section series B, nos. 41—57; section series C, nos. 81—91; section series D, nos. 1—14; pls. 21, 28, 45, 49). In the *Cephalaspis*-species it then passes latterally in the interspace of the lateral part of the visceral endoskeleton falling between the canals sel_1 and sel_2 (text-figs. 23, 24, 46, 47; pls. 28, 29). In *Boreaspis*, *Hoelaspis* and *Kiaeraspis* it would of course be expected to be situated beneath the preorbital part of the canal $sel_{1,2}$, which, as we have found, was traversed by both the first and second nerves to the lateral electric field, but instead of that it goes in these forms always behind the said part of the canal $sel_{1,2}$ and the canal sel_2 (text-fig. 28; pls. 14, 44, 49, 50, 55, 57) — a fact which, if we assume the conditions in the *Cephalaspis*-species to be the primitive ones, indicates that the canal sel_2 has moved forwards and fused with the canal sel_1, which has retained its original position. Conditions similar to those in *Boreaspis*, *Hoelaspis* and *Kiaeraspis* probably prevailed also in *Benneviaspis*. Finally it deserves to be mentioned that the canal for the trigeminus proper, when laterally to the orbit it crosses the canal $sel_{1,2}$ on the lower side, for a rather long distance may be in open communication with that canal (section series A, nos. 119—155; section series B, nos. 43—45, 53—56). The facialis canal (VII), though it leaves the vestibular division of the labyrinth cavity postero-dorsally to the canal sel_3 for the third nerve to the lateral electric field (text-figs. 18, 19; section series A, nos. 72—110; section series C, nos. 87—105), has such a course that is soon arrives on the anterior side of this canal, which it follows rather close until it opens into the oralo-branchial chamber (text-figs. 28, 46, 47; section series A, nos. 72—110; section series B, nos. 28, 29, 34—51; section series C, nos. 87—105; pl. 20; pl. 23, fig. 3; pls. 25—29, 44, 45, 49, 50, 57). Somewhat antero-ventro-laterally to the labyrinth cavity it may often be fused with the canal sel_3 for a certain distance (section series A, nos. 85—107; section series B, nos. 28, 29, 39—41; section series C, nos. 97—101; section series E, no. 21). The glossopharyngeus canal (IX*a*) issues from the vestibular division of the labyrinth cavity either between the canals sel_4 and sel_5 or just dorsally to the canal sel_5 (text-figs. 18, 19, 23—25, 27, 28; section series A, nos. 65—97). During its way antero-laterally it crosses the canal sel_4 on the ventral side, then continuing anteriorly to this and thus in the interspace between the canals sel_3 and sel_4 until it opens into the oralo-branchial chamber (text-figs. 4, 13, 28, 36, 46, 47; pls. 28—30, 44, 49, 50, 57). The canal for the first branchial branch of the n. vagus, X_{br_1}, seems, at least in certain forms as *Kiaeraspis* (text-fig. 28; pl. 52), to have gone so that its distal end was situated almost beneath the proximal part of the canal sel_5; and the nerve transmitted by it must evidently have passed antero-ventro-laterally between the canals sel_4 and sel_5 though not within but ventrally to the visceral endoskeleton. The second branchial branch of the n. vagus had, as we have seen, no canal of its own, but entered the oralo-branchial chamber associated with one or two of the branchial branches behind it. But as, like the other branchial nerves in front, it must have gone downwards along the medial side of the interbranchial septum 5, it certainly had its course between the canals sel_5 and sel_6, though, like the first branchial branch of the same nerve, it went medially to the visceral endoskeleton.

We thus see that each one of the six nerves to the lateral electric field during its passage through the visceral endoskeleton went more or less close posteriorly to a branchial nerve. And we are thus able to establish that the nerves to the lateral electric field alternated in a regular way with the branchial nerves, and that therefore, like these, they had a distinct metameric disposition. In this connection it should be emphasized that in *Boreaspis*, *Hoelaspis*, and *Kiaeraspis* the position of the second electric nerve for the lateral electric field in front of the n. trigeminus proper presumably was a secondary character.

Since the aortal groove, as we have seen, stretches forwards with its most anterior portion on the internal surface of the rostral part of the visceral endoskeleton as far as the point at which the prebranchial ridge meets and unites with its fellow of the other side, it is fully clear that the aorta reached forward to that point and that it was a single trunk throughout its cephalic division.

Each of the interbranchial ridges 1 and 2 of *Kiaeraspis* (text-figs. 4, 36; pl. 51) and each of the interbranchial ridges 1—3 of *Hoelaspis* (pl. 44; pl. 46, fig. 1) has a groove in its longitudinal direction for an efferent branchial artery, a groove which stretches from the oartal groove more or less far laterally. The anterior interbranchial ridges of the other Cephalaspids are very imperfectly known with regard to details and thus we cannot know whether, as a rule, they had similar grooves for the anterior efferent branchial arteries or not. Accordingly it is so far impossible to decide whether these grooves did generally occur among the Cephalaspids or whether their presence in *Kiaeraspis* and *Hoelaspis* was quite an exception[1].

The groove for the first efferent branchial artery (*a. eff*$_1$) is in *Kiaeraspis* (pl. 51) rather short, being limited only to about the dorso-medial fourth of the interbranchial ridge 1. In *Hoelaspis* (pl. 44; pl. 46, fig. 1) it is

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[1] In text-fig. 13, which is a diagrammatic sketch of a *Cephalaspis*-species, grooves for efferent branchial arteries have been drawn on the interbranchial ridges 1—3. It must, however, be noticed that this is arbitrary and that these grooves have not been observed in any *Cephalaspis*-species known so far. It should also be pointed out that the groove for the rostral artery (*a. rostr*) in the same figure has also not been observed in *Cephalaspis*-species.

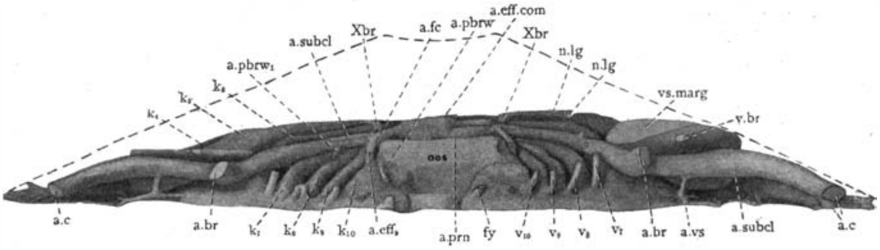
somewhat longer, occupying almost the entire dorso-medial third of the corresponding interbranchial ridge. Both in *Kiaeraspis* and in *Hoelaspis* its most medial part which leads into the aortal groove (*aort. gr*) is curved rather much backwards, so that it does not meet the aortal groove at right angle, but somewhat obliquely. The groove for the second efferent branchial artery (*a.* eff_2) is in *Kiaeraspis* very short, being distinctly developed only in the vicinity of the aortal groove. In *Hoelaspis,* on the contrary, it is much longer, extending approximately along the entire dorso-medial half of the interbranchial ridge 2. Both in *Kiaeraspis* and in *Hoelaspis* its most medial part which joins the aortal groove curves backward like that of the first one. Otherwise it is noticeable that in *Hoelaspis* it is rather wide. The groove for the third efferent branchial artery (*a.* eff_3), which, as has already been stated, has been found so far only in *Hoelaspis*, occupies in the specimen figured in pl. 44 in which it is best known approximately the dorso-medial third of the interbranchial ridge 3, and it is thus shorter than the second one. On the other hand, it is wider than that and does not curve as much backwards. It joins the aortal groove somewhat behind the place at which the carotid canals issue, and on the whole it is situated on the anterior part of the orbital prominence (*pr. orb*) and thus on the lower surface the endocranium.

From the description now given of their grooves and from the figures it is easy to see that the three most anterior efferent branchial arteries must have passed between the first and second, the second and third and the third and fourth gill-sacs respectively. Accordingly each of these three arteries seems, as far as can be judged, to have arisen from the adjacent halves of two neighbouring gill-sacs, quite as the efferent branchial arteries in *Petromyzon* (GOODRICH 1909, text-fig. 32; CORI 1906, pp. 29—30; HATTA 1922, pp. 135—150). In *Myxine*, on the contrary, each efferent branchial artery has its origin only from one gill-sac. It is further of importance to notice here that in *Hoelaspis* the rather considerable lateral extension of the grooves for the three efferent branchial arteries in question seems to indicate that the gill-sacs there did not stretch so very far medially, but that the pharynx probably was rather wide.

Before we proceed further in our account of the efferent branchial arteries we shall consider the unpaired median ridge denoted *r. eff. com* in the figures, a ridge which has already been referred to above. This ridge (text-figs. 4, 33; section series F, nos. 1—28) is, as has already been pointed out, situated on the anterior surface of the postbranchial wall, dorsally to the oesophagus, and belongs to the portion of the postbranchial wall, that bridges over the aortal groove ventrally, transforming this in the aortal canal. In its interior it contains a longitudinal canal (*a. eff. com*, text-figs. 9, 10, 36, 39, 40, 45; section series F, nos. 1—28; pl. 28; pl. 46, fig. 1; pl. 47, fig. 1; pls. 51, 52; pl. 53, figs. 2, 3; pl. 58), a canal which thus is situated below the aortal groove and which anteriorly opens into that groove approximately as far forward as between the middle parts of the otic prominences (*pr. au*). Posteriorly, it seems to have ended somewhat above the dorsal border of the oesophagus foramen, just anteriorly to the pronephros space; and the wall which separated it from that space was probably very thin. According to the inclined position which the ridge *r. eff. com* occupies, the posterior end of the canal *a. eff. com* lies considerably lower than the anterior one. As will be evident from the facts given below, that canal lodged an artery which arose by the confluence of certain of the posterior efferent branchial arteries and which may therefore be called the arteria branchialis efferens communis. This artery (text-fig. 45) thus ascended to and opened from the ventral side into the cephalic division of the dorsal aorta.

To the canal just described for the arteria branchialis efferens communis there lead, at least in *Cephalaspis hoeli*, from each lateral side three foramina or very short canals ($a.\ eff_4$—$a.\ eff_6$, text-fig. 33; section series F, nos. 7—25). The most anterior one of these foramina or short canals ($a.\ eff_4$) perforates the ridge (*r. eff. com*) near the anterior end, opposite the interbranchial ridge 4. The one, $a.\ eff_5$, of them following next posteriorly lies behind the middle of the length of the ridge *r. eff. com*, opposite the interbranchial ridge 5, whereas the third and most posterior one, $a.\ eff_6$, pierces the ridge *r. eff. com* rather close behind the second one, opposite the interbranchial ridge 6. From their position and relations it is not difficult to understand that these three foramina or short canals transmitted the efferent branchial arteries 4—6, and that these three efferent branchial arteries therefore must have gone along but somewhat ventrally to the interbrancihal ridges 4—6 (text. fig. 41), so that, as a rule, there arose no grooves for them on those ridge. And we thus find that the efferent branchial arteries 4—6 had their passage between and arose from two neighbouring gill-sacs, exactly like the three ones in front.

From the posterior part of the canal for the arteria branchialis efferens communis a paired wide canal (*a. subcl*, text-figs. 36, 39, 40; section series C, nos. 60—123; section series F, nos. 11—48; pls. 20, 22; pl. 24, fig. 2; pl. 28; pl. 46, fig. 1; pl. 47, fig. 1; pls. 51, 52; pl. 53, figs. 2, 3; pl. 58) issues in a lateral and postero-ventral direction through the postbranchial wall. More closely defined, this canal goes first almost straight laterally just behind the interbranchial ridge 6, then curving more downwards and laterally, so that almost during the rest of the way to the ventral part of the postbranchial wall it passes behind the interbranchial septum 6. On the posterior surface of the ventral part of the postbranchial wall it causes the formation of a considerable ridge which is designated in the figures by the letters *r. subcl*, thus the ridge that has been referred to already above under the term of the



Text-fig. 40. *Cephalaspis hoeli.* Cast of the ventral half of the posterior part of the oralo-branchial chamber with certain of the canals of the postbranchial wall, of the endoskeletal shoulder-girdle and of the cornua. Restoration made after section series F. Magnification about 4/1.

a. br, canal for the arteria brachialis; *a. c,* canal for the arteria cornualis; *a.* eff_9, canal for the efferent branchial artery 9; *a. eff. com,* canal for the artera branchialis efferens communis; *a. fc,* groove for an artery arisen by the confluence of the two most posterior efferent branchial arteries; *a. prn,* canal for an artery to the pronephros space; *a. pbrw—a.* $pbrw_1$, canals for the arteries to the posterior side of the postbranchial wall; *a. subcl,* canal for the arteria subclavia; *a. vs,* canal for a ventral superficial artery to the ventral side of the shield immediately in front of the pectoral sinus; *fy,* canal probably for a ventral superficial longitudinal vein; k_4—k_{10}, branchial fossa 4—10; *n. lg,* canal probably for the n. lineae lateralis; *oes,* division of the oesophagus-truncus-arteriosus foramen for the oesophagus; *v. br,* canal probably for the vena brachialis; *vs. marg,* marginal vein sinus (dorsal parts imperfect); v_7—v_{10}, canals for the ventral transversal superficial veins 7—10; X_{br}, canal for the most posterior branchial branches of the n. vagus.

subclavian ridge. From the ventral part of the postbranchial wall the paired canal in question continues into the basal parts of the endoskeletal shoulder-girdle, where soon after its entrance its gives off a thick branch posteriorly or postero-laterally to the medial part of the pectoral sinus, a branch (*a. br,* text-figs. 35, 36, 39, 40; section series C, nos. 117—119; section series F, nos. 34—44; pl. 52; pl. 54; fig. 2) which undoubtedly went to the pectoral fin. Laterally to this branch it takes a more straight lateral direction through the endoskeletal shoulder-girdle until it enters the cornu, within the most antero-medial part of which it bifurcates into two main branches, a posterior one (*a. c,* text-figs. 35, 36, 39, 40; section series C, nos. 124—130; section series F, nos. 49—59) which curves backwards into the ventro-medial part of the cornu of its side, within which it can be traced very far backwards, and an anterior one (*a. marg,* text-figs. 36, 39; section series C, nos. 124—127 section series F, nos. 49—66; pls. 20, 22, 44, 51) which takes an anterior direction along the very lateral margin of the shield, where, at least in *Kiaeraspis,* it goes forwards until slightly in front of the branchial fossa 2, joining there the canal denoted by the letters *v. marg.* Somewhat before its entrance into the cornu its gives off a branch (*a. vs,* text-fig. 40; section series F, nos, 43—60) which goes down to the ventral side of the shield in front of the pectoral sinus. And as is well shown by text-fig. 39, both the branch (*a. c*) to the cornu, which will be called the cornual branch, and the anterior branch along the margin of the shield (*a. marg*), which will be termed the marginal branch, send out numerous fine rami. The latter branch is in communication medially by small rami with the canal *v. marg*.

The canal *a. subcl*, as thus described, must obviously have been traverved by an artery, an artery which was in communication dorso-medially with the arteria branchialis efferens communis and which supplied the pectoral fin, the shoulder-girdle, the cornu and by far the larger part of the lateral margin of the shield latero-ventrally to the lateral electric field. According to its origin, course and area of supply this artery may very well have been homologous with the arteria subclavia of fishes (DANIEL 1922, pp. 173—174; 197—199; ALLEN 1905, pp. 46, 49—51, 63—65, 115; LUCAS 1905, pp. 104—105; etc.); and it will therefore be referred to as the subclavian artery and its canal as the subclavian canal. Of the branches of the subclavian canal the one (*a. br*) to the pectoral fin evidently transmitted an artery which, at least with regard to funtion, seems to have corresponded to the brachial artery of fishes (DANIEL, loc. cit; ALLEN, loc. cit; etc.), while the branch to the lower side of the shield (*a. vs*) was traversed by an artery which may have been the equivalent of one of the superficial branches which are given off from the artery in recent fishes that is called by ALLEN (1905, pp. 49—51) the ventral artery and by DANIEL (1922, pp. 167—169) the coracoid artery. Since it perforated the endoskeletal shoulder-girdle in a ventral direction and supplied the ventral superficial parts of the shield, I suggest here for it the name of ramus superficialis ventralis of the a. subclavia. The marginal branch (*a. marg*) of the subclavian canal lodged an artery which is to a certain extent suggestive of the artery of fishes described by DANIEL (1922, loc. cit.) as the coracoid artery [thus the most anterior part of the ventral artery of ALLEN'S description (1905 loc. cit.) of the *Loricati*], but which, on account of its position dorsally to the external branchial openings, cannot have been homologous with that. According to its position in the cephalic shield it will here be termed the arteria marginalis. Finally the cornual branch (*a. c*) of the subclavian canal gave passage to an artery which may perhaps be thought to have been simply an enlarged superficial branch of the arteria subclavia or of the arteria coracoidea of fishes. In the subsequent account we shall call this artery of the Cephalaspids the arteria cornualis. Accordingly we find that the arteria subclavia of the Cephalaspids gave off an arteria brachialis and a ramus superficialis ventralis and that it then divided into two chief branches: the arteria marginalis and the arteria cornualis. And accordingly it was in many important features very much like the a. subclavia of fishes.

In *Cephalaspis hoeli* (text-figs. 33, 41; section series F, nos. 26—44) each of the interbranchial septa 7—9 has, on the dorsal half of its posterior surface close to the medial edge, a distinct groove which leads upwards to the opening of a canal situated in the post-branchial wall. The most anterior one of these grooves is thus situated on the anterior side of the branchial fossa 8, the second on the anterior side of the branchial fossa 9, and the most posterior one on the anterior side of the branchial fossa 10. The canal, *a. eff*$_7$, into which the most anterior one leads, has its ventral opening at the very dorsal end of the branchial fossa 8, close behind the upper end of the interbranchial septum 7 and thus approximately at the point at which this septum passes over into the interbranchial ridge 7. The ventral openings of the canals, *a. eff*$_8$, *a. ff*$_9$, into which the remaining two grooves lead, have a quite corresponding position in relation to the branchial fossae 9 and 10 and to the interbranchial septa 8 and 9 respectively. Since, however, the branchial fossa 8 is slightly higher than the interbranchial fossa 9, and this last than the interbranchial fossa 10, the ventral opening of the most anterior one of the three canals lies of course slightly higher than that of the second and that of the second in its turn slightly higher than that of the most posterior one.

The most posterior one of these canals (*a. eff*$_9$ text-figs. 33, 34, 36, 39, 40, 41; section series F, nos. 24—34) goes from the oralo-branchial chamber upwards through the postbranchial wall close antero-laterally to the line of origin of the pronephros lamella (*p. nl*) of its side. Rather soon during its passage upwards it meets and joins with the canal *a. eff*$_8$, which also ascends within the postbranchial wall. The common canal formed by the union of the canals *a. eff*$_8$ and *a. eff*$_9$, which is lettered *a. fc* in the figures (text-figs. 33—36, 39, 40; section series F, nos. 16—24), continues upwards, curving slightly medially and opening into the dorso-medial part of the canal for the arteria subclavia, thus rather close to the canal for the arteria branchialis efferens communis. Finally the canal *a. eff*$_7$ (text-figs. 33, 36, 39, 40, 41; section series F, nos. 19—26) goes almost straight upwards through the postbranchial wall, opening from the ventral side into the canal for the arteria subclavia close ventro-laterally to the canal *a. fc*. The dorsal part of the canal *a. eff*$_9$, the entire canal *a. fc* and a more or less long part of the canal for the arteria subclavia, ventro-laterally to the canal *a. fc* are, as has already been pointed out (pp. 148—149), in *C. hoeli* without bony covering on the posterior side. In that form when alive, however, the said canals were bridged over at these places by the periost.

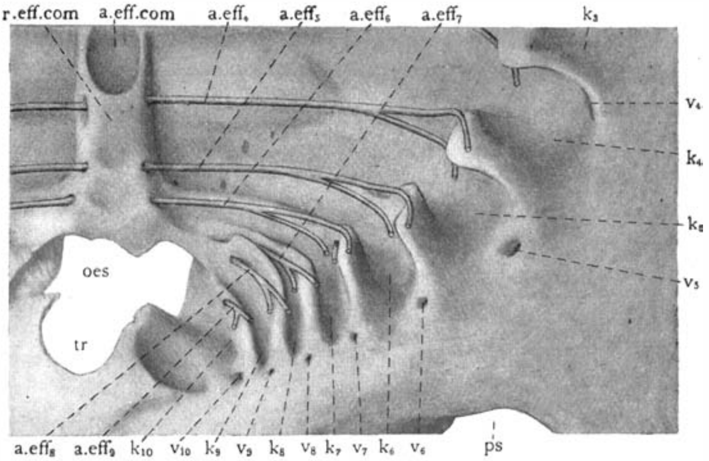
From their position and course it is easy to conclude that the canals *a. eff*$_7$, *a. eff*$_8$ and *a. eff*$_9$ now described, and the grooves leading to these canals from below, must have lodged the three most posterior efferent branchial arteries — that is the efferent branchial arteries 7, 8 and 9. And we thus find here that these arteries emptied into the arteria subclavia, as we have defined that artery above. It deserves to be specially pointed out, however, that the proximal part of the last-mentioned artery, medially to the point at which the arteria branchialis efferens 7 opened into it, probably had arisen by the union of the dorsal ends of the arteriae branchialis efferentes 7—9, and consequently that this part would strictly not be ascribed to it. Concerning the arteria subclavia it is in this connection also of interest to notice that, at least in certain fishes, e. g. the Selachians (DANIEL 1922, p. 197), it is given off from the dorsal aorta between the posterior efferent branchial arteries, and that it thus also in fishes may have similar relations to the efferent branchial arteries as in the Cephalaspids.

Since the grooves for the efferent branchial arteries 7, 8 and 9 ventrally to the canals within the postbranchial wall reach down to the medial margins of their respective interbranchial septa, it is very conceivable that the three efferent branchial arteries 7—9, like the six ones in front, arose by the confluence of branches from two adjacent gill-sacs, and thus that the conditions with regard to all the efferent branchial arteries were as in the Petromyzontids. How I imagine the three most posterior efferent branchial arteries to have gone in relation to the interbranchial septa is shown by text-fig. 41.

At least in *Cephalaspis hoeli* there is a rather fine canal lettered *a. eff*$_{6p}$ in the figures (text-figs. 11, 12, 33, 41; section series F, nos. 30—35), which, from the branchial fossa 7, ascends upwards through the interbranchial septum 6 to the canal for the a. subclavia. This canal *a. eff*$_{6p}$ seems, as far as can be judged from its position and course, to have given passage to an artery, which carried blood from the anterior half of the gill-sac 7 into the a. subclavia. And accordingly it seems as if the efferent branchial artery 6 had brought blood chiefly only from the posterior half of the gill-sac 6.

Finally attention should be called to the fact that in other Cephalaspids, such as *Hoelaspis* (pl. 47, fig. 1) and *Kiaeraspis* (pl. 58), the canals for the efferent branchial arteries 7—9 probably were almost exactly as in *C. hoeli*, though their posterior walls probably were entirely ossified.

After the efferent branchial arteries proper have thus been dealt with a few remarks must be made on the rostral artery, thus the artery lodged in the groove on the prebranchial ridge (*a. rostr*, text-figs. 4, 36; pl. 51). As has already been pointed out, it is quite evident that this artery was in communication with the anterior end of the dorsal aorta posteriorly. And as it seems to have been serially homologous with the efferent branchial arteries behind, and as it went in the anterior wall of the first gill-sac, it is very likely that it recieved the blood from the anterior half of that gill-sac and thus was the premandibular efferent branchial artery.



Text-fig. 41. *Cephalaspis hoeli*. Sketch showing how the three most posterior efferent branchial arteries probably arose from two neighbouring branchial fossae. Magnification about 8/1.

a. eff$_4$ — *a. eff*$_9$, efferent branchial arteries 4—9; *a. eff com*, canal for the arteria branchialis efferens communis. For the lettering in general see text-fig. 33.

The dorsal field of the external surface of the visceral endoskeleton was, in the rostral part, supplied with arterial blood by branches from the a. facialis, more exactly by the anterior branches, by the mandibular branch and by the lateral infraorbital branch from that artery. And as the canals of these branches have already been dealt with above in the description of the ethmoidal region, only a few remarks remain here to be added concerning them. As is well shown by text-figs. 28, 44, 46, 47 and certain of the plates (pls. 27, 28, 45, 49, 55) the canal or canals for the first one or the first ones of these branches passed on the portion of the rostral part of the visceral endoskeleton situated anteriorly or antero-medially to the canal for the n. profundus (V_1). And as is also obvious from the figures and plates cited (cf. also pls. 29, 30) the canal for the mandibular branch (*a. am*) had its course on the portion of the visceral endoskeleton between the canal for the n. profundus (V_1) and that for the n. trigeminus proper (V_2), while the canal for the lateral infraorbital branch (*a. iol*) went on the portion of the visceral endoskeleton falling between the canals for the n. trigeminus proper (V_2) and that for the n. facialis (VII). Accordingly we find that the branches of the a. facialis to the dorsal field of the external surface of the visceral endoskeleton had a rather distinct metameric disposition. Finally, it should be pointed out that, as is well seen from their canals, the mandibular and lateral infraorbital branches of the a. facialis went down to and supplied the anterior parts of the lateral electric field.

The dorsal field of the outside of the visceral endoskeleton behind the orbit received its arterial blood generally from four superficial arteries, the dorso-lateral superficial arteries 1—4. The canals for these arteries (*a. sa*, *a. sm*$_1$, *a. sm*$_2$ and *a. sp*) are often very distinctly displayed in the specimens (text-figs. 28, 44, 46—48, 49; pls. 20, 23, 25, 27, 29, 30, 39 44, 47, 49, 50, 55), and it is easily ascertained that the first one (*a. sa*) lies above the interspace between the canals for the n. facialis (VII) and the n. glossopharyngeus (IX *a*), that the second (*a. sm*$_1$) and third (*a. sm*$_2$) ones have their position above the interspace between the canals for the n. glossopharyngeus and the first branchial branch of the n. vagus (X_{br_1}), while the remaining one (*a. sp*) presubably goes above the interspace between the first and second branchial branches of the n. vagus. It is also clearly seen that the canals for the dorso-lateral superficial arteries alternated in a rather regular way with the canals (*sel*$_1$—*sel*$_6$) for the nerves to the lateral electric field. And there can be no doubt, therefore, that the dorso-lateral superficial arteries 1—4, like the anterior and lateral branches of the a. facialis, had a metameric arrangement. We are thus able to establish the very interesting fact that all the chief dorsal superficial arteries had a metameric arrangement. It should further be mentioned here that, as their canals reached down to the lateral electric field, the four dorso-lateral superficial arteries carried blood inter alia also to the lateral electric field.

As we have found, the canals for the dorso-lateral superficial arteries issue from the dorso-lateral part of the vestibular division of the labyrinth cavity (text-figs. 18, 19, 23, 25, 26; section series A, nos. 54—92; section series B, nos. 1—38; section series C, nos. 81—107; section series D, nos. 1—10; pls. 17, 18, 23—25, 44). But while in certain cases they are rather independent of each other throughout their extent, they may in other cases unite with each other and with neighbouring canals in the vicinity of the labyrinth cavity. And owing to this the number of canals for dorsolateral superficial veins issuing from the labyrinth cavity is, as we already have seen (pp. 87—90 above), subjected to considerable variations.

Before we leave the canals for the dorso-lateral superficial arteries, it deserves to be mentioned that either from the proximal part of the fourth one (*a. sp*) or from the common canal (*a. slcm*) arisen by the fusion on the fourth with the third one of these canals, there issues a rather considerable branch in a postero-lateral direction (text-fig. 48; pl. 25), a branch which, in its turn, soon divides into several finer branches. It seems very likely that the dorso-lateral superficial arterial branch transmitted by it represented either a fifth dorso-lateral superficial artery or a number of posterior vestigal dorso-lateral superficial arteries.

In many of the specimens it is distinctly seen that all the canals for superficial branches from the a. facialis, the canals for the dorso-lateral superficial arteries, the canals for superficial branches from the marginal and cornual arteries, the canals for the ventral superficial branch of the a. subclavia as well as the canals for the arteries to the dorsal side of the endocranium on the external surface of the endoskeleton — that is to say between the exo- and endoskeleton — break up into a very great number of fine branches which anastomose with each other, forming a plexus of canals, a plexus of canals that lodged the subaponeurotic vascular plexus pls. 25, 39; pl. 40, fig. 5; pl. 45) already referred to above (pp. 34, 35). And we thus find that the subaponeurotic vascular plexus received blood from the superficial branches of the a. facialis, from the dorso-lateral superficial arteries, from the postorbital superficial artery and other superficial arteries on the dorsal side of the endocranium, and in addition from the marginal and cornual arteries and the r. superficialis ventralis of the a. subclavia.

On the posterior surface of the postbranchial wall we find the openings of certain fine canals which issue from the the canal for the arteria subclavia, the canal for the efferent branchial artery 9 and the canal for the arteria branchialis efferens communis. These fine canals, the two most important of which are denoted in the figures (text-figs. 34—35; 39, 40), by the letters *a. pbrw* and *a.* $pbrw_1$, evidently transmitted arteries to the postbranchial wall, particularly to the posterior side of that. The postbranchial wall thus received its arterial blood from the a. subclavia, from the most posterior efferent branchial arteries, and from the arteria branchialis efferens communis.

Between the subclavian ridge (*r. subcl*) antero-medially and the endoskeletal shoulder-girdle postero-laterally there, is in all Cephalaspids, a paired rather wide opening (pls. 9, 14, 15; pl. 47, fig. 1, pl. 52; pl. 53, figs. 2, 3) which leads antero-laterally into a big paired cavity lettered *vs. marg* in the figures. This cavity (text-figs. 9—12, 34—36, 39, 40; section series A, nos. 156, 165—167; section series C, nos. 108—122; section series F, nos. 24—55; pls. 15, 22; pl. 23, fig. 3; pls. 51, 52, 58) is bounded postero-laterally by the endoskeletal shoulder-girdle, medially by the lateral part of the postbranchial wall and the most posterior portion of the lateral part of the visceral endoskeleton, and is situated above the distal part of the canal for the arteria subclavia, very close laterally to the branchial fossae 5 and 6. Both in *Cephalaspis hoeli* (text-figs. 9—12, 34, 39; section series F, nos. 29—41; pls. 20, 22) and in *Kiaeraspis* (text-fig. 36, pl. 51, 52) it opens anteriorly by means of a rather narrow foramen into a wide canal *v. marg*, whereas in certain other forms such as *Boreaspis rostrata* (pl. 15) it seems to pass over rather gradually into that canal. Into the antero-ventro-medial part of it open two short canals v_5 and v_6 (text-fig. 34; section series C, nos. 111—115; section series F, nos. 38—53; pls. 10, 20, 22), which ascend from the most basal parts of the branchial fossae 5 and 6; and to its postero-dorsal part there leads a short canal (*v. br*, text-figs. 9—11, 34, 35, 39, 40; section series C, nos. 119—122; section series F, nos. 28—33; pl. 10) from the dorsal part of the pectoral sinus.

The canal *v. marg* (text-figs. 11, 12, 36, 39; section series A nos 157—158; section series B, nos. 1, 6; section series C, nos. 117—126; section series F, nos. 29—62; pls. 15, 20, 22, 44, 51, 52, 58), if for a detailed examination we next turn to that, is situated in the most ventral portion of the lateral part of the visceral endoskeleton of each side, close laterally to the lowest part of the oralo-branchial chamber, and reaches from the cavity *vs. marg* forwards until just opposite the basal part of the branchial fossa 1. As a whole, it narrows rather much forwards, though not gradually, as a rule, the parts of it situated just opposite the interbranchial septa 1—3 being in most cases considerably widened in proportion to the parts of it which lie just opposite the basal parts of the branchial fossae 2—4. Expressed in another way, it has a swelling situated laterally to each of the interbranchial septa 1—3 (text-figs. 36, 39; pl. 51), though it gets as a whole a smaller diameter forwards. It is in communication by means of the short canals v_1—v_4 (text-figs. 4, 36; section series C, nos. 112—121; section series F, nos. 38—49; pls. 22, 51) with the most ventral parts of the branchial fossae 1—4 and by means of several fine branches with the canal for the marginal artery (*a. marg*) which lies close laterally to its three posterior fourths and opens into it with the anterior end just opposite the anterior basal part of the branchial fossa 2.

Behind the cavity *vs. marg*, we find the basal parts of the postbranchial wall, on each side of the median line, perforated by four, short fine canals v_7—v_{10}. More closely defined, these short canals ascend from the most basal parts of the branchial fossae 7—10 in a dorso-postero-lateral direction to the ventral part of the posterior surface of the postbranchial wall (text-figs. 4, 33, 34, 35, 36, 39, 40, 41; section series C, nos. 85—110; section series F, nos. 39—58; pls. 9, 10, 20, 22, 51; pl. 53, fig. 3; pl. 58). In view of both their course and their position, they must beyond question be serially homologous with the canals v_1—v_6, in front, which open into the canal *v. marg* and the cavity *vs. marg*. In several cases two neighbouring ones among the posterior four of these canals have been found to unite with each other during their course to the posterior surface of the postbranchial wall, so that not rarely they may open on this surface only with two or three openings (see text-figs. 39, 40 and pl. 10).

Somewhat laterally to the most ventral part of the foramen for the truncus arteriosus (*tr*) or the homologoue of that, if there is a single big oesophagus-truncus-arteriosus foramen, a paired canal, lettered *fy* in the figures (text-figs. 4, 33, 34, 35, 36, 39, 40; section series F, nos. 54—58; pls. 9, 10, 20), pierces the most ventral part of the postbranchial wall from the posterior to the anterior surface. The opening of that canal on the last-mentioned surface lies slightly lower than that on the other and, as is well shown by text-fig. 33, in addition somewhat medially to the ventral part of the branchial fossa 10. At least in the species of *Cephalaspis hoeli* used for section series F (nos. 54—57) there was close antero-medially to the canal *fy* a second, though much finer, canal (*fz*), which also perforated the postbranchial wall from the posterior to the anterior surface.

Owing to its position just medially to the canal for the marginal artery and to its width and shape otherwise, we can hardly be in doubt that the canal *v. marg* and the cavity *vs. marg* lodged a big vein, which was widened between the branchial fossae. This vein which, on account of its position in the cephalic shield, may be termed the marginal vein, certainly continued for some distance postero-medially behind the ventral part of the postbranchial wall above the canals v_7—v_{10} of its side; and it seems beyond question that the vessels which were lodged in these canals, as well as those which traversed the canals v_1—v_6, opened into it. The canals v_1—v_{10} were thus, as far as we can judge, traversed by transversally running veins, which came from the superficial parts of the ventral side of the branchial region. These veins may be called the vv. superficiales transversales ventrales.

On account of their position, distribution and connections with each other, it is not difficult to see that the v. marginalis and the ventral superficial transversal veins correspond respectively to the v. longitudinalis dorsalis and the main parts of the system of transversal superficial veins of the Petromyzontids (text-fig. 99; cf. CORI 1906, pp. 56—63; pl. 11, pl. 12, fig. 3; HATTA 1922, pp. 195—202). The canal *fy* already described was probably traversed by a vein which may have corresponded to the vena seperficialis longitudinalis ventralis of the Petromyzontids, and it will therefore be referred to as the canal for the vena superficialis longitudinalis ventralis. The ventral transversal superficial veins probably were in communication ventrally with the vena superficialis longitudinalis ventralis. The marginal vein received several small superficial tributaries from the lateral margin of the shield and from the ventral rim, and both it and the vena superficialis ventralis may in their turn have united and emptied into the vena jugularis ventralis. How I imagine the marginal vein, the ventral transversal superficial veins, and the ventral longitudinal superficial vein to have been situated is further elucidated by the restoration given in text-fig. 50. And as we find, it is not difficult to see that the Cephalaspids had a superficial vein system which was very suggestive of that in Petromyzontids.

The anterior fourth of the canal *v. marg* was conceivably traversed not only by the marginal vein but also by the most rostral part of the marginal artery, for, as we have seen, the canal for that artery joins with and opens into the canal *v. marg* anteriorly opposite the branchial fossa 2. Anteriorly to the canal *v. marg*, as above defined, the rostral artery may probably have continued forwards through the canal *va*, (text-figs. 4, 36; section series F, nos. 45, 49; pl. 51), and it is not improbable that, most anteriorly within that canal it was continuous with and passed over into a fine anterior branch of the truncus arteriosus. The canal *va*, would thus if the opinion now advanced is true have been an arterial canal. But the possibility is not to be entirely denied, however, that instead it may have transmitted a vein, and since it opens into the oralo-branchial chamber with its anterior end it would in such a case with this end be serially homologous to the canals v_1—v_{10} and would allude to that there perhaps primarily had been still one branchial fossa anteriorly to the premandibular one which is now the most anterior one found.

The venous blood from the most antero-medial portion of the dorsal field of the external surface of the visceral endoskeleton was usually to a great extent collected into superficial veins, which went forwards towards the rostral end of the region, uniting during their course forwards into wider veins. The canals of this vein-system, which will be called the rostral vein-system, vary much in number, extent and course in different forms. They go all forwards until somewhat posteriorly to the rostral margin, where they curve downwards and penetrate into the interior of the region, opening there into a thick canal, the rostral vein sinus (*vs. r*, text-figs. 36, 50; section series C, in several of the figures between the numbers 2—100; section series F, nos. 39, 42, 49; pls. 44, 45, 51), which runs concentrically with the anterior margin of the cephalic shield. This vein sinus, into which there also open several canals from the rostral margin, reaches on each side of the median line as far postero-laterally as somewhat behind the prebranchial ridge, there turning backwards and opening into the oralo-branchial camber very close above the oralo-branchial fenestra and slightly in front of the anterior orifice of the canal *va*.

For the detailed study of the canals for the rostral vein-system we first turn to *Kiaeraspis* and *Hoelaspis*, and after these to the *Cephalaspis*-species.

In *Kiaeraspis* (text-figs. 28, 36, 50; pls. 49, 51) the medial canals of the rostral vein-system arise from the subaponeurotic plexus far back on the rostral part of the visceral endoskeleton, in fact close in front of the nasal aperture. During their course forwards these medial canals join each other, forming in this way a rather thick median rostral vein canal (*v. rm*) which goes forwards to the rostral vein sinus. The lateral canals (*vv. rs*), on the contrary, arise much less forwards and do not join very much with each other, but generally they go as independent canals to the rostral vein sinus. Owing to the fact that the median superficial portions of the rostral part of the visceral endoskeleton thus were chiefly drained by the rostral vein-system, the tributary branches to the canal for the vena capitis lateralis have, as we shall find, only a rather slight extension in these portions.

Hoelaspis seems in most respects to resemble *Kiaeraspis* very much with regard to the system of rostral vein canals (pls. 44, 45), but the median canals, however, do not join each other until close behind the rostral vein sinus.

In the genus *Cephalaspis* the system of rostral vein canals seems to exhibit rather great variations in different species. As a rule, however, it seems to be less developed here and to extend less far backwards with its medial canals than in the two genera already dealt with. Not rarely it may be asymmetrical in arrangement. In *C. vogti*, in which it is best known (text-fig. 47; pl. 27), its canals on each side of the median line unite with each other, but while in this way there is formed on the left side a chiefly longitudinal trunk (*v. rl*) there arises instead on the right side a trunk (*v. rh*) concentrically with the anterior edge of the shield. Unlike in *C. vogti* the rostral vein canals of *C. spitsbergensis* seem to have gone forwards rather independent of each other (text-fig. 49; pl. 39). Unfortunately, however, they are very imperfectly known in that species. Finally in a *Cephalaspis*-specimen, probably pertaining to *C. arcticus* (text-fig. 51; pl. 40, fig. 5), the system of rostral veins must have been restricted only to a very narrow zone along the rostal margin of the region, for, as is distinctly seen, the vein canals on the antero-medial parts of the upper side of the region all go backwards, joining the canal for the right vena capitis lateralis, which in this way is very much extended forwards and much more strongly developed than its fellow of the left side. The veins on the upper side of the region of this specimen are thus very asymmetrical in their arrangement.

The usually big vein which was lodged in the rostral vein sinus was postero-ventrally probably continued by a semicircular vein which was situated within the soft tissue laterally and posteriorly to the mouth opening; and there is thus much reason to believe that there was an annular vein sinus around the mouth, as in Cyclostomes. This annular vein sinus was perhaps in communication with the ventral longitudinal superficial vein of each side (text-fig. 50).

The part of the subaponeurotic vascular plexus of the dorsal side of the visceral endoskeleton behind the one from which the rostral vein system arose was drained by six veins, the dorso-lateral superficial veins, which all ascended to and emptied into the v. capitis lateralis. The canals for these veins — the four posterior ones of which have already been dealt with rather much in detail above (pp. 75—76) — are those which are lettered $v.\ ls_1$—$v.\ ls_6$ in the figures (text-figs. 23—28, 46—51; section series C, nos. 66—113; pls. 17, 18, 20, 24—30, 39, 40, 41, 45; pl. 47, fig. 1; pls. 49, 50, 53, 55).

The most anterior one, *v. ls_1*, of these canals is always situated on the dorsal part of the visceral endoskeleton slightly medially to the canal for the n. profundus (V_1). As a rule, it is rather short and narrow; but in certain forms in which the rostral veins, particularly the lateral ones, have only a rather slight extension backwards, it is developed more in length forwards, so that in these forms the vein lodged by it drained a much larger area of the subaponeurotic vascular plexus than was otherwise the case. And in the specimen of *C. arcticus* figured in text-fig. 51, and pl. 40, fig. 5 in which, as has been pointed out, the rostral veins are very short, extending only slightly behind the rostral vein sinus, the right canal for the first dorso-lateral superficial vein, as has also been remarked, has increased very much in length and is in communication with canals for the rostral veins — conditions which evidently suggest that the dorso-lateral superficial vein 1 of the right side was very strong and drained by far the greater portion of the subaponeurotic vascular plexus on the rostral part of the visceral endoskeleton. The canal for the dorso-lateral superficial vein 1 always opens into the canal *v. cl_1* for the preorbital division of the v. capitis lateralis.

The dorso-lateral superficial vein canal following next backwards, that is the one lettered *v. ls_2*, reaches with its most ventro-lateral branches into the lateral electric field. As a rule, it passes first dorso-medially and slightly posteriorly on the portion of the visceral endoskeleton between the canals for the n. profundus and the n. trigeminus proper, then curving more medially or antero-medially and uniting with the canal *v. cl_1* for the preorbital division of the v. capitis lateralis, more or less far behind the canal *v. ls_1*. In most cases it has to cross the canal for the n. profundus in order to reach the canal *v. cl_1*, and its dorso-medial portion therefore partly falls on the rostral part of the vicseral endoskeleton.

The canals for the dorso-lateral superficial veins 3—6, like the second one just described, can all be traced down into the lateral electric field. Of them the third one from in front, *v. ls_3*, passes above the interspace that was limited by the n. trigeminus proper and the n. facialis, the fourth one, *v. ls_4*, above the interspace that was limited by the n. facialis and the n. glossopharyngeus, the fifth one, *v. ls_5*, above the interspace that was limited by the n. glossopharyngeus and the first branchial branch of the n. vagus, and finally the sixth one, *v. sl_6*, behind the last-mentioned space. And it is thus clear that these four canals for dorso-lateral superficial veins also alternated with the nerves and had a metameric arrangement. Accordingly we find that the dorso-lateral superficial veins in fact represented the dorsal portion of a system of metamerically arranged transversal veins, the ventral portion of which was constituted by the ventral transversal superficial veins. It is very likely that the dorso-lateral superficial veins, by means of very fine branches, reached even ventro-laterally to the lateral electric field and were in communication with the marginal vein.

How the canals for the four posterior dorso-lateral superficial veins went in their most dorso-medial portions and how with these portions they joined each other in different ways in different forms has already been fully dealt with above on pp. 75—76, to which the reader is referred for further details concerning them.

From the accounts given of the vascular canals of the visceral endo-skeleton we have been able to establish that the Cephalaspids had in the head a system of superficial arteries and veins with a very distinct metameric arrangement. And as this metameric arrangement also is in accord with the metameric arrangement of the branchial nerves and branchial sacs, we find that branchiomery, neuromery, and vasomery in the head were all in complete agreement with each other.

Before we leave the visceral endo-skeleton it should be noticed that in one specimen of *Kiaeraspis* the upper surface of the oralo-branchial chamber, on the orbital prominence and somewhat anteriorly to this, has two paired series of short obliquely transversally arranged grooves. The detailed appearence of these series of grooves is well shown in text-fig. 36 and in pl. 51. What their function might have been I have so far not been able to ascertain.

Cranial nerves.

As in the account given above the different nerves of the head have been dealt with in connection with the description of their canals, and thus not at all coherently, it may be of importance to give here a summary of what can be concluded concerning their components and course.

Spino-occipital nerves must have been present in all *Cephalaspidae*. In the *Cephalaspis*-species and in the Cephalaspids with a short occipital region they were at least two (text-figs. 32, 43), but never more than three. In *Kiaeraspis* and in other forms with a long occipital region, on the other hand, they probably always exceeded that number. As is fully evident from the position of their canals (nv_1, nv_2, nd_1, nd_2, *etc.*, text-figs. 15—17, 20—27, 28; pls. 18, 19; pl. 23, fig. 3; pl. 44; *spi*, pl. 53, fig. 1) through the lateral wall of the occipital region they alternated with each other in such a way that each one of those on the right side left the cavum cerebrale cranii slightly in front of the corresponding one of those on the left side. In this respect therefore they vere like the spinal nerves of *Amphioxus* and the recent Cyclostomes (text-fig. 38). In addition, it seems as if they all had dorsal and ventral roots, and as if these roots had not united but passed off separately, without uniting into a spinal ganglion, quite like the dorsal and ventral roots of the spinal nerves of *Amphioxus* and *Petromyzon*.

Like the spino-occipital nerves, the spinal nerves of the right and left sides certainly also alternated with each other, and their dorsal roots probably also did not unite with their ventral ones. And as far as can be judged therefore the Cephalaspids, with regard both to the spino-occipital and spinal nerves, presented conditions which otherwise are found only among the *Cephalochordata* and *Cyclostomata*.

The roots of the n. glossopharyngeus and of the n. vagus as well as the roots of the metaotic lateralis nerves all left the cavum cerebrale cranii through a common canal, the vagus canal. In several cases they remained probably during their entire passage through this canal closely or rather closely associated with each other (IX + X, textfigs. 20—22, 28), in other cases the glossopharyngenus-roots diverged more or less from the vagus roots and emerged from the cranial wall by a branch (IX, text-figs. 15—17, 23, 24, 26) of their own of the vagus canal, a branch which is termed the glossopharyngeal branch.

The vagus roots became ganglionic probably already within the distal part of the vagus canal, but the main part of their ganglionic complex seems to have been situated just externally to the cranial wall, posteriorly to the postbranchial wall. More exactly, the chief part of their ganglionic complex probably occupied a rather distinct pit on the upper part of the posterior surface of the postbranchial wall (text-fig. 14), a pit, which perhaps in many cases may have been imperfectly bridged over posteriorly by bone.

Of the branchial branches of the n. vagus the first one arose from the ganglionic complex close externally to the vagus canal. Immediately after its origin it turned antero-ventro-laterally and went into the canal X_{br_1} (text-fig. 4, 13, 28, 33, 34, 39; section series A, nos. 62—65; section series C, nos. 79—86; section series E, nos. 7—12; section series F, nos. 2, 3; pls. 28, 52, 57) through the ventral wall of the otic region below the vestibular division of the labyrinth cavity to the oralo-branchial chamber, which it reached rather far dorso-medially in the branchial fossa 5, more or less close laterally or postero-laterally to the otic prominence. Already during its passage through the ventral wall of the otic region it gave off a rather strong branch ventrally to the dorso-medial part of oralo-branchial chamber, a branch which traversed a canal of its own (X_{br_1v}, pl. 52) and which certainly must have supplied the pharynx and which therefore, as far as can be judged, consisted of communis fibres. According to its course and position, this branch seems to have been homologous with the visceral branch of the corresponding branchial branch of the n. vagus in Petromyzontids (cf. text-fig. 38; Johnston 1905, pp. 187—189). During its further course ventrally the first branchial branch of the n. vagus probably passed chiefly medially to the interbranchial septum 4. The other branchial branches of the n. vagus certainly always took their origin from the ganglionic complex more distally to the vagus canal. Associated into two or three trunks, they passed downwards and slightly posteriorly, and, after having pierced the upper medial part of the postbranchial wall by two or three short canals (X_{br_2}—X_{br_6}, X_{brp}, X_{br}, text-figs. 14, 33, 34, 36, 39, 40), they entered the postero-dorso-medial part of the oralo-branchial chamber posteriorly to the otical prominence. In that chamber they must rather soon have separated from each other and have passed down to the medial sides of their respective interbranchial septa, that is to say the interbranchial septa 5—9. It is also presumable that, like the branchial nerves in front, all of them had a visceral branch (text-fig. 43).

The ramus intestinalis vagi, if it was present, must have been given off from the vagus ganglionic complex rather straight backwards. The n. lineae lateralis probably rather soon laterally to the vagus canal took a postero-lateral direction across the most dorsal portion of the posterior surface of the postbranchial wall in order to reach the main lateral line.

From what is known so far concerning the n. vagus it is evident that it was not exclusively composed of communis and viscero-motor fibres, but that it also had general cutaneous and lateralis components.

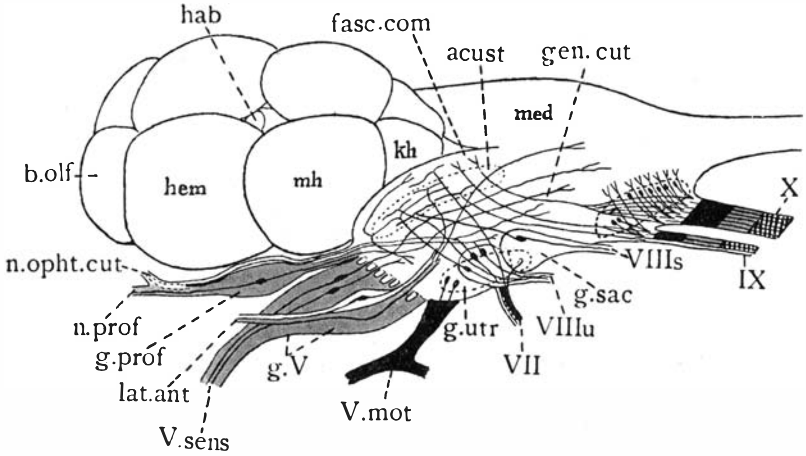
Probably the glossopharyngeus roots did not become ganglionic until after their exit from the vagus canal; and since they left the cranial wall close dorsally to the vagus roots, their ganglia may presumeably have been situated slightly dorsally to the pit in which the chief part of the vagus ganglionic complex had its position. Accordingly we find that the glossopharyngeus roots too emerged and probably had their ganglia posteriorly to the postbranchial wall. After its origin from the ganglia the n. glossopharyngeus went first for a short distance laterally along the posterior surface of the otic region, then it turned forwards and, after having pierced the posterior wall of the otic capsule through the canal IX*p* (text-figs. 18, 19, 26, 28; section series D, nos. 3—7; pl. 25), it traversed the postero-lateral corner of the vestibular division of the labyrinth cavity. From there it continued antero-latero-ventrally through the canal IX*a* (text-figs. 4, 18, 19, 23, 24, 25, 27, 28, 36, 43, 46, 47; section series A, nos. 65—97; section series B, nos. 18—25; section series C, nos. 95—109; pls. 20, 28—30, 44, 49—51, pl. 54, fig. 1; pl. 62, fig. 1; pl. 57) to the oralo-branchial chamber, which it reached antero-laterally to the orbital prominence in the branchial fossa 3, probably always rather close dorso-medially to the interbranchial septum 3. In *Kiaeraspis* (text-fig. 36, pl. 51) the conditions of the canal IX*a* show clearly that the n. glossopharyngeus close, before its entrance into the oralo-branchial chamber, divided into two chief branches, one of which went antero-ventrally, probably along the anterior border of the interbranchial septum 3, whereas the other took a postero-ventral course conceivably along the posterior border of the same interbranchial septum. As the last-mentioned one of these branches sent fine rami to the exoskeleton externally to it, it must evidently have consisted of general cutaneous fibres. And as this is the case, it follows of course that the antero-ventrally running branch must have consisted of viscero-motor fibres for the innervation of the visceral musculature situated in the interbranchial wall between the gill-sacs 3 and 4. In any case it is hardly probable that the antero-ventrally running branch could have been a pretrematic branch, but that this branch was absent.

In certain forms (pl. 28) a rather wide branch (IX_{av}) could be observed leaving the canal IX*a* on the ventral side, rather close laterally to the vestibular division of the labyrinth cavity. As this branch went to the dorso-medial part of the oralo-branchial chamber, the nerve-branch transmitted by it certainly was the serial homologoue of the similarly situated one of the first branchial branch of the n. vagus, and, like that, it probably supplied the pharynx. This nerve branch seems thus to have consisted of communis fibres and would obviously have been the r. visceralis of the n. glossopharyngeus. As far as can be judged, therefore, the n. glossopharyngeus of all the Cephalaspids had a visceral branch, though, owing to the state of preservation of most forms it is usually impossible to prove its occurence.

The n. glossopharyngeus must have consisted of communis fibres, viscero-motor fibres, general cutaneous fibres and probably also of lateralis fibres.

Within the cavum cerebrale cranii the glossopharyngeus-vagus roots might perhaps be thought to have been accompanied by special electric fibres for the lateral and dorsal electric fields, and if it was so certain of these fibres — those for the dorsal electric field — would have left the cavum cerebrale cranii through the canal *dx*, (text-figs. 15, 17—20, 22, 23, 26; section series A, nos. 49—52), whereas the others — those for the lateral electric field — would have passed to the labyrinth cavity associated with the n. glossopharyngenus. It seems more probable, however, that no special electric fibres for the electric fields had their exit from the cavum cerebrale more or less close in relation to the glossopharyngeus-vagus roots, but that the canal *dx* instead gave passage either to a nerve of general cutaneous fibres from the glossopharyngeus or vagus or to a lateralis branch from one of the metaotic lateralis nerves. It may also be thought that this canal, in addition to a nerve consisting of general cutaneous or lateralis fibres or of both, transmitted also an artery. Finally it is also possible that the canal *dx* was a mere arterial canal and had nothing at all to do with dorsal nerve branches from the n. glossopharyngeus or the n. vagus. Which of all these alternatives was true it is impossible to say at present.

The n. acusticus probably divided already within the cavum cerebrale cranii into two branches, a ramus posterior and a ramus anterior. The r. posterior left the cavum cerebrale throught the canal VIII*p* (text-figs. 15—17, 18, 19, 20—22, 24, 28, 32, 43; section series A, nos. 57—59;



Text-fig. 42. *Myxine.* Diagram of the components of the cranial nerves after N. HOLMGREN 1919.

acust, acusticum; *b. olf*, bulbus olfactorius; *fasc. com*, fasciculus communis; *g. prof*, profundus ganglion; *g. V*, ganglion gasseri; *g. sac*, ganglion sacculare; *g. utr*, ganglion utriculare; *gen. cut*, general cutaneous tract; *hab*, habenular ganglion; *hem*, hemispheres; *kh*, cerebellum; *lat. ant*, n. lateralis anterior; *med*, medulla oblongata; *mh*, mesencephalon; *n. ophth. cut*, n. ophthalmicus cutaneous; *n. prof*, n. profundus; *V. mot*, viscero-motor root of the n. trigeminus proper; *V. sens*, sensorial part of the n. trigeminus proper; VII, n. facialis; VIIIs, VIIIu, ramus saccularis and ramus utricularis respectively of the n. acusticus; IX, n. glossopharyngeus; X, n. vagus.

section series D, nos. 4—9; pls. 25, 26, 49, 50) and entered the postero-ventro-medial corner of the vestibular division of the labyrinth cavity close antero-ventrally to the ampulla posterior. From its mode of entrance into the labyrinth cavity we may be justified therefore in concluding that it supplied the ampulla posterior and certain parts of the vestibulum, just as the corresponding branch of the recent Cyclostomes. The r. anterior, which probably was thicker than the r. posterior, had its exit from the cavum cerebrale cranii through the canal VII+VIII*a* (text-figs. 15—22, 24, 28; section series A, nos. 63—70; section series B, nos. 19—25; section series C, nos. 41—52; section series D, nos. 2—19; pls. 14, 18; pl. 19, fig. 1; pl. 23, fig. 3; pls. 24—26, 45, 47, 49, 50, 55) together with the roots of the n. facialis, the prootic lateralis roots and the roots of the special nerves to the electric fields, and entered the vestibular division of the labyrinth cavity close to the bottom and somewhat ventrally to the ampulla anterior. According to ist course and mode of entrance into the labyrinth cavity, it must evidently have innervated the ampulla anterior, the anterior parts of the vestibulum and the commisure.

As was pointed out just above, the roots of the n. facialis, the roots of the prootic lateralis nerves and the roots of all, or at least of the majority of, the nerves to the electric fields traversed, on their way outwards from the cavum cerebrale cranii, the canal VII+VIII*a* together with the n. acusticus. All of them thus entered the vestibular division of the labyrinth cavity; and those of the n. facialis seem to have become ganglionic immediately after their entrance there. More exactly, their ganglia may have been situated close to, or on the bottom of, the proximal part of the vestibular division of the labyrinth cavity. The n. facialis proper, after its origin from its ganglion, traversed the basal parts of the vestibular division of the labyrinth cavity and, leaving it between the canals sel_3 and sel_4 (text-figs. 4, 13, 18, 19, 23, 24, 25, 27, 28, 36, 46—48; section series A, nos. 72—112; section series D, nos. 9—14; pls. 23—29, 44, 45, 49, 50, 51, 54, 55, 57), continued through the canal VII to the oralo-branchial chamber, which it reached more or less far laterally in the branchial fossa 3. Since the canal VII has a branch (VII_v, pl. 23, fig. 3; pl. 44) which seems to be serially homologous with the branch of the canal IX*a*, which was considered to have transmitted the visceral branch of the n. glossopharyngeus, it is very likely that the n. facialis too had a visceral branch. From the conditions of the canal VII in *Cephalaspis heintzi* (pl. 29) and in *Kiaeraspis* (text-fig. 36; pls. 51, 55, 57) it is obvious that the n. facialis gave off branches to the superficial parts of the cephalic shield and that most distally, just before or at its entrance into the oralo-branchial chamber exactly as the n. glossopharyngeus, it broke up into two main branches which went along the interbranchial septum 3. Just as in the case of the n. glossopharyngeus, the anterior one of these branches must have consisted of viscero-motor fibres, while the posterior one was composed of general cutaneous fibres. A pretrematic branch was, as far as can be judged, entirely absent. From what is known so far of its canal therefore it is easy to conclude that the n. facialis was not exclusively composed of viscero-motor and communis fibres but that it also had a component of general cutaneous fibres and perhaps also one of lateralis fibres. That a general cutaneous component was present in this nerve is a very interesting feature, since such a component otherwise is known with certainty in it only among the Petromyzontids (cf. Johnston, 1905, pp. 185, 198).

The lateralis roots which entered the labyrinth cavity together with the facialis roots were probably two in number (text-figs. 32, 43). It seems likely that one of them became ganglionic already shortly after reaching the labyrinth cavity, and that the nerve which arose from the ganglion thus formed traversed the vestibular division of that cavity accompanying the n. facialis at least for some distance distally in order to reach certain sensory organs of the lateral line system laterally to the otic region. The other root, on the contrary, immediately after its entrance into the labyrinth cavity, turned antero-laterally and reached the orbit after traversing the canal *l* (text-figs. 18, 19, 24, 28, 43;

section series A, nos. 71—93; section series B, nos. 22—31; section series C, nos. 49—66; section series D, nos. 1—3, 8—10; pls. 14, 18; pl. 19, fig. 1; pl. 23, fig. 3; pls. 25, 26, 49, 50, 55). It probably became ganglionic just after its entrance into the orbit. And as far as can be understood, its ganglion was, therefore, situated on the bottom of the orbit, close laterally to the myodome and postero-laterally to the ganglion gasseri. Of the two chief nerves which arose from this ganglion one went forwards, probably at least for a certain posterior stretch accompanying the n. profundus, while the other associated with the n. trigeminus proper must have passed first along the lateral part of the bottom of the orbit and then further antero-ventro-laterally in the canal V_2. During its course within the orbit the latter nerve probably gave off several branches laterally through certain or all of the canals *bu* and bu_1—bu_4 (text-figs. 24, 28; section series A, nos. 105, 109, 115; section series B, nos. 29, 31—33, 37, 38, 43, 46, 49; section series C, nos. 85—89; section series D, nos. 1—3, 14—19; pls. 28, 45, 49, 50); and, as far as can be judged from its course and mode of branching, it thus seems to have corresponded to the n. buccalis lateralis of fishes.

With regard to their relations to the labyrinth cavity, the n. facialis and the prootic lateralis fibres must obviously have been almost exactly as in the recent Petromyzontids (AHLBORN 1883, pp. 259—272; JOHNSTON 1905, pp. 157—163; 1908).

The roots of the nerves for the electric fields were probably very strong and certainly occupied a conciderable part of the canal VII + VIIIa during their passage to the labyrinth cavity. If they had any ganglionic formations, which cannot be positively decided, these formations must have been situated in the medial portion of the vestibular division of the labyrinth cavity, probably on or close to the bottom. Be this as it may, however, it is quite certain that their fibres rather soon after their entrance into the labyrinth cavity, divided into two groups, a lateral one which followed the floor of the vestibular division of the labyrinth cavity laterally, and a dorsal one which went upwards into the dorso-medial parts of the labyrinth cavity.

The lateral one of these two groups in its turn soon broke up into six thick nerves which all traversed the vestibular division of the labyrinth cavity and had their exits from this through the canals $sel_{1,2}$, sel_3, sel_4, sel_5 and sel_6 (text-figs. 18, 19, 23—28, 34, 43, 46—48; section series A—F; many of the plates especially, however, pls. 21, 27, 29, 30, 44, 45, 49, 50), in which they continued to the lateral electric field. These nerves, which, in view of their function will be referred to as the lateral electric nerves thus, after they had left the endocranium, perforated a considerable part of the visceral endoskeleton. Most of them did not branch until — or rather close before — their entrance into the lateral electric field. The most posterior one, which was lodged in the canal *sel*$_6$ always had a postero-lateral course. Most laterally it perforated the dorsal part ot the endoskeletal shoulder-girdle (text-figs. 13, 34). The next one forwards, that is to say the one which was transmitted by the canal *sel*$_5$, left the vestibular division of the labyrinth cavity just behind or just postero-ventrally to the n. glossopharyngeus and went rather straight laterally to the lateral electric field. The third one from behind, i. e. the one which passed through the canal *sel*$_4$, always had a lateral and somewhat anterior direction and crossed the n. glossopharyngeus on the dorsal side somewhat laterally to the anterior half of the labyrinth cavity. The fourth one, still counted from behind, accordingly the one which had its passage through the canal *sel*$_3$, went antero-laterally until it reached the lateral electric field. It crossed the n. facialis on the ventral side rather close antero-laterally to the labyrinth cavity. Finally, the two most anterior ones both turned forwards within the vestibular division of the labyrinth cavity and entered and traversed the canal *sel*$_{1,2}$ closely associated with each other. Thus they passed first forwards close laterally to the orbit and crossed the n. trigeminus on the dorsal side. In the *Cephalaspis*-species the canal *sel*$_{1,2}$, as we have seen, reaches only as far forwards as just anteriorly or antero-laterally to the orbit, dividing there into the branches *sel*$_1$ and *sel*$_2$ which diverge from each other and go antero-laterally to the anterior parts of the lateral electric field. And in view of these conditions it is obvious that the two most anterior lateral electric nerves in the *Cephalaspis*-species most anteriorly or antero-laterally to the orbit turned more laterally, diverged from each other and went separately during the rest of their course to their area of supply. In *Hoelaspis* (pl. 45), *Boreaspis* (pl. 14), and *Kiaeraspis* (pls. 49, 50), on the contrary, as is obvious from the extension of the canal *sel*$_{1,2}$, the two nerves in question went associated with each other still further than in the *Cephalaspis*-species, in *Boreaspis* and *Kiaeraspis* even to or almost to their entrance into the lateral electric field. How all the six lateral electric nerves branched within the lateral electric field is well shown by text-fig. 28 and by pls. 21, 30, 50 and by pl. 31, fig. 3; and we shall have the opportunity of returning to this matter below in the special description of the electric fields.

Before we leave the lateral group of electric nerves the fact deserves to be emphasized that these nerves alternated in a certain regular way with the ordinary branchial nerves and that accordingly they had a metameric arrangement (text-figs. 43, 46, 47).

The dorsal group of electric nerve fibres, immediately after separating from the lateral group, went upwards and slightly postero-medially in the groove *dsv* on the medial side of the labyrinth cavity (text-figs. 18, 19; section series A, nos. 50—60; section series B, nos. 18—23; section series C, nos. 1, 23—40; section series D, nos. 17—36). In the upper part of this groove — that is to say in the upper part of the commissural division of the labyrinth cavity — they rather suddenly turned dorso-medially, or in certain cases dorso-medially and slightly posteriorly, and entered the wide canal *des* (text-figs. 18, 19, 23, 26, 27; section series A, nos. 50—60; section series B, nos. 18—23; section series C, nos. 1, 23—40; section series D, nos. 17—36). After having traversed this canal they reached the dorsal electric field, within which they branched very frequently and anastomozed with those of the opposite side. How the branching took place is well displayed by the specimens figured in pls. 17, 29 and 39.

From their course in relation to the n. facialis and its roots it seems not improbably that the electric nerves described here for the chief parts of the electric fields were in reality a specialized part of the n. facialis. In this respect, therefore, the Cephalaspids would have been somewhat suggestive of *Torpedo*, in which the first electric nerve is a part of the n. facialis (cf. DANIEL 1922, p. 553).

Concerning the n. abducens very little can be ascertained. All that can be said of it is that — if it existed as an independent nerve — it may probably have emerged into the myodome together with the viscero-motor root of the n. trigeminus proper.

The n. trigeminus proper and the n. profundus were very independent of each other; and for that and other reasons to be given below, they will here be treated separately.

In *Cephalaspis hoeli* and at least in several other *Cephalaspis*-species too, the n. trigeminus proper arose from two roots — a ventral one which consisted of viscero-motor fibres, and a dorsal one which was chiefly made up of general cutaneous fibres but which in addition probably also had communis fibres intimately associated with it. The ventral root, which on its way out from the cavum cerebrale cranii traversed the canal V*d* (text-figs. 16, 17, 24, 43; section series A, nos. 70—86; section series B, nos. 19—29; section series C, nos. 1—9, 35—41; pl. 18; pl. 19, fig. 1; pl. 21; pl. 23, fig. 3; pls. 25, 26) must have left the medulla oblongata very low and close antero-ventrally to the acustico-facialis roots, approximately as the viscero-motor root of *Myxine* (text-fig. 42; cf. HOLMGREN 1919). It emerged into the external part of the myodome. The dorsal root, which was transmitted from the cavum cerebrale cranii by the canal V*c* (text-figs. 16, 17, 24, 43; section series A, nos.; 79—84; section series B, nos. 28, 29; section series C, nos. 33—48), obviously left the medulla oblongata somewhat antero-dorsally to the ventral root. Like that, it went to the external part of the myodome, which, however, it, entered more dorsally and often also more laterally than that.

Conditions very similar to those now described in *Cephalaspis hoëli* and other *Cephalaspis*-species with regard to the trigeminus roots proper and their exits probably occurred also in *Hoelaspis* (pl. 45) in *Boreaspis* (pl. 14) and in *Thyestes verrucosus* (pl. 48, fig. 1).

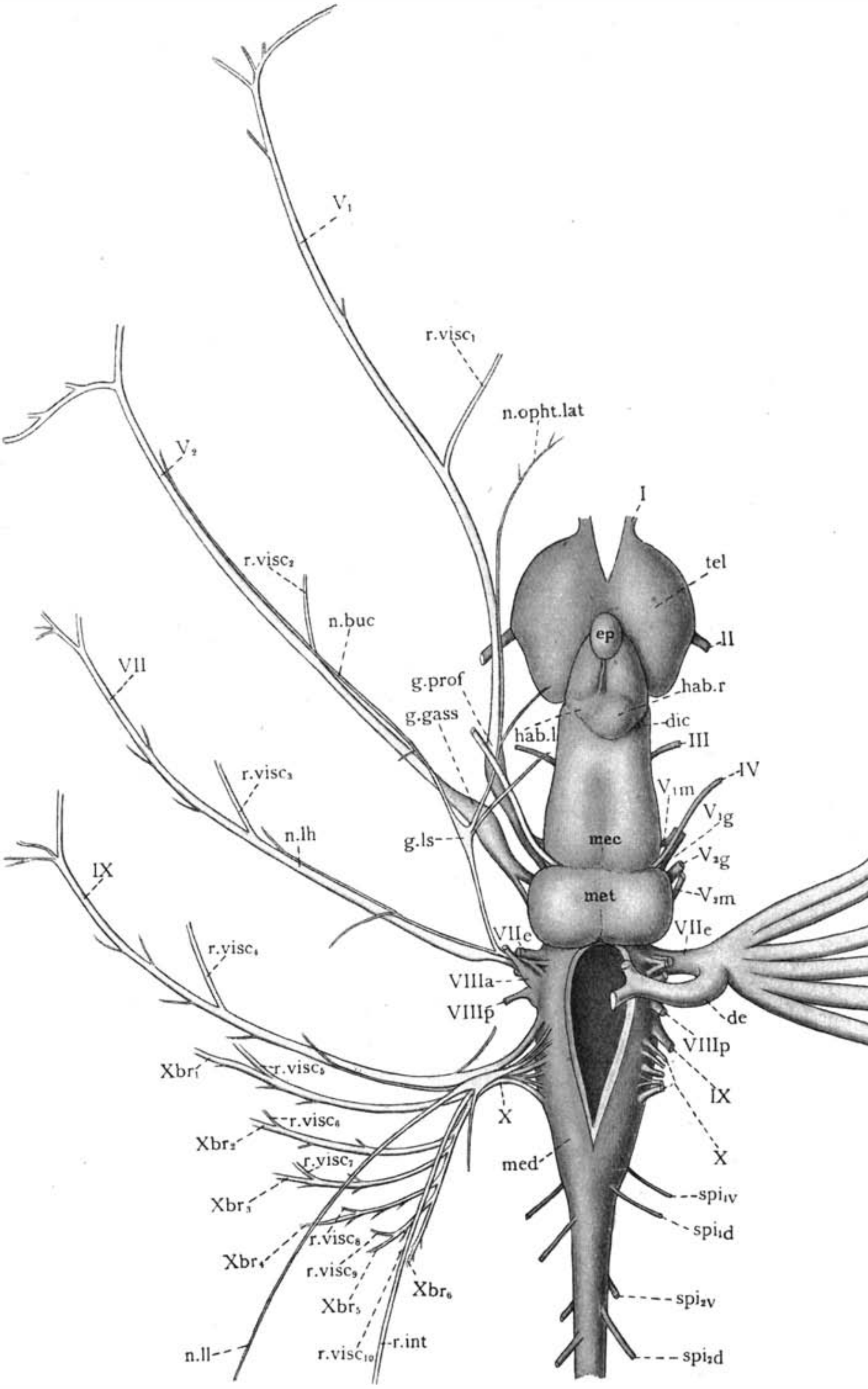
In *Kiaeraspis* also the n. trigeminus proper probably arose from the medulla oblongata by two similar roots as in the other forms, but the two roots, at least in several cases, did not perforate the cranial wall separately but through a common canal (V, text-figs. 20—22, 28; section series D, nos. 2—14; pls. 49, 50, 55); a canal which in addition transmitted the roots of the n. profundus too. With regard to the place of entrance of the trigeminus roots into the myodome *Kiaeraspis* seems in all essential points to have been quite like the other Cephalaspids.

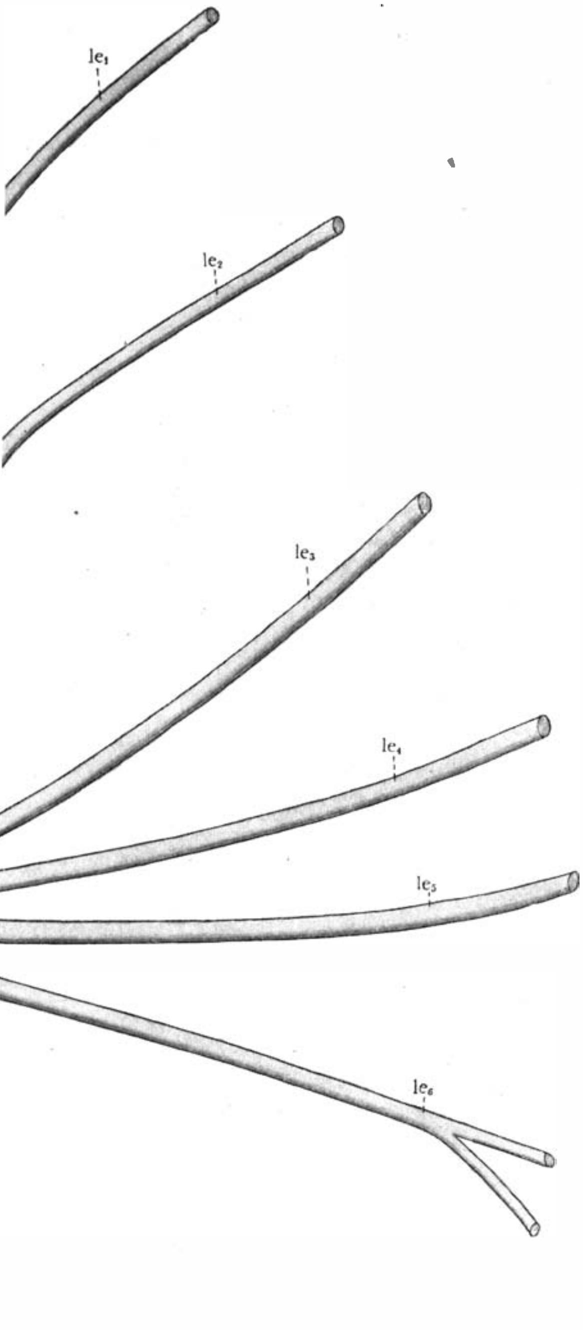
In all Cephalaspids the dorsal trigeminus root had at least a big ganglion gasseri formed by the general cutaneous fibres, and possibly there was also a communis ganglion. The latter, if it existed, however, was probably more or less intimately united with the former. For the sake of brevity, however, we shall here refer to the possibly somewhat compound ganglionic structure of the dorsal trigeminus root only as the ganglion gasseri. From the course of the dorsal trigeminus root it is quite clear that the ganglion gasseri, in that somewhat wide sense, was chiefly situated in the postero-ventro-medial part of the orbit, but that in addition with a small medial part it reached medially into the external (lateral) part of the myodome. In relation to the lateralis ganglion formed by the fibres which entered the orbit through the canal *l* it lay at least chiefly antero-dorso-medially.

In all Cephalaspids the trigeminus proper, after its origin from the ganglion gasseri went antero-laterally close to the floor of the orbit and was, as has already been pointed out above (p. 195), during this part of its course as well as farther distally for a considerable stretch accompanied by a lateralis nerve, which must have corresponded to the n. buccalis lateralis of fishes and Petromyzontids. It left the orbit rather far anteriorly through the canal V_2 (text-figs. 4, 13, 24, 25, 28, 36; section series A, nos. 122—155; section series B, nos. 41—55; setion series C, nos. 81—91; pl. 14; pl. 19, fig. 1; pl. 21; pl. 23, fig. 3; pls. 28, 29, 45; 49, 50, 51; pl. 54; fig. 1; pls. 55, 57, 58) and, after traversing this canal — whithin which probably branches issued from it to the superficial parts of the cephalic shield — it definitely arrived into the oralo-branchial chamber in the lateral (ventro-lateral) part of the branchial fossa 2, close dorso-medially to the interbranchial septum 1. Like the n. glossopharyngeus and the n. facialis, it gave off a ventral branch to the dorso-medial part of the oralo-branchial chamber, a branch which seems to have gone to the anterior portion of the pharynx and which therefore, as far as can be judged, was a visceral branch. The canal for this visceral branch is the one denoted V_{2v} in the plates (pl. 23, fig. 3; pl. 28). Rather far distally to its supposed r. visceralis, and at or close before its exit into the oralo-branchial chamber, the canal for n. trigeminus proper, at least in *Kiaeraspis* (text-fig. 36; pl. 51), gave off an antero-ventral branch towards the anterior border of the upper end of the interbranchial septum 1, while the chief part of it went postero-ventrally and divided into several rami, which continued downwards on the medial side and along the posterior border of the same interbranchial septum. And we thus find that its mode of branching at the dorsal end of its interbranchial septum was on the whole very much like that of the other branchial nerves nearest behind, and it is therefore very likely that the anterior branch, as in these nerves, was composed of viscero-motor fibres and that this branch accordingly could not have been a pretrematic branch. A further support for this opinion is the fact that it does not seem very probably that the anterior branch could have crossed the entire branchial fossa 1. With regard to the remaining portion of the n. trigeminus proper that passed to the medial side and the posterior border of the interbranchial septum 1, it is of course probable that this, like the corresponding portion of the n. facialis and the n. glossopharyngeus, consisted only of general cutaneous fibres; but owing to its considerable size, however — combined with the fact that the visceral musculature within the interbranchial wall 1, since this wall corresponded to the velum, probably was stronger than in the other interbranchial walls — it is rather likely that, in addition to these fibres, it also included a component of viscero-motor fibres. The presence of a special velum nerve could not be established.

As is shown by its mode of branching, it is thus quite clear that the n. trigeminus proper was composed of communis fibres, visceromotor fibres and general cutaneous fibres; but besides these it was also, for a considerable stretch, accompanied by a nerve of lateralis fibres. Moreover the n. trigeminus proper was certainly in most essential points of a similar simple type as the branchial nerves behind it, but in its mode of branching distally, however, it seems to have been somewhat more specialized than these. Finally attention should be called to the fact that, if, as I suppose, its posterior portion had a viscero-motor component, it would with regard to its branching have been rather suggestive of the corresponding nerve in the Petromyzontids (cf. text-fig. 38; JOHNSTON 1905, pl. 5).

The n. profundus certainly had in all Cephalaspids a rather thick root which consisted chiefly of general cutaneous fibres, but which in addition had intimately joined with it a number of communis fibres. This root, which for the sake of brevity will be referred to as the general cutaneous root, always went to the most dorso-lateral part of the myodome, slightly antero-dorsally to the dorsal (general cutaneous-communis) root of the trigeminus proper. In *Cephalaspis hoeli* (text-figs. 15—17; section series A, nos. 78—93; section series B, nos. 30—37; section series C, nos. 29—42), and probably also in several other species, it traversed during its passage to the myodome the cranial wall through a canal of its own (V*b*). In *Kiaeraspis*, on the contrary, it


V_1
r.visc$_1$
n.opht.lat
V_2
I
tel
r.visc$_2$
n.buc
ep
II
g.prof
hab.r
g.gass
hab.l
dic
III
VII
r.visc$_3$
V_1m
IV
n.lh
V_1g
g.ls
mec
V_2g
IX
met
V_3m
VIIe
VIIe
r.visc$_4$
VIIIa
VIIIp
de
VIIIp
Xbr$_1$
r.visc$_5$
IX
X
r.visc$_6$
Xbr$_2$
X
med
r.visc$_7$
spi$_1$v
Xbr$_3$
spi$_1$d
r.visc$_8$
Xbr$_4$
r.visc$_9$
Xbr$_6$
Xbr$_5$
spi$_2$v
r.int
n.ll
r.visc$_{10}$
spi$_2$d



Text-fig. 43. Restoration of the brain and cranial nerves of a Cephalaspid. Dorsal view. On the left side the ordinary cranial nerves, on the right side the the electric nerves.

de, electric nerve to the dorsal electric field; *dic*, diencephalon; *ep*, epiphysis; *g. gass*, ganglion gasseri; *g. ls*, lateralis ganglion situated in the orbit; *g.prof*, profundus ganglion; *hab. l*, left habenular ganglion; *hab.r*, right habenular ganglion; le_1—le_6, electric nerves to the lateral electric field; *mec*, mesencephalon; *med*, medulla oblongata; *met*, cerebellum; *n. buc*, nervus buccalis lateralis; *n. lh*, lateralis nerve which perhaps accompanied the n. facialis; *n. ll*, n. lineae lateralis; *n. ophth. lat*, n. ophthalmicus lateralis; *r. int*, r. intestinalis vagi; *r.* $visc_1$—*r.* $visc_{10}$, supposed visceral branches of the branchial nerves; $spi_{1\,d}$—$spi_{2\,d}$, dorsal roots of the first and second spino-occipital nerves respectively; $spi_{1\,v}$, $spi_{2\,v}$, ventral roots of the first and second spino-occiptal nerves respectively; *tel*, telencephalon; I, n. olfactorius; II, n. opticus; III, n. oculomotorius; IV, n. trochlearis; V_1, n. profundus; V_{1g}, general cutaneous (+ communis) root of the n. profundus; V_{1m}, viscero-motor root of the n. profundus; V_2, n. trigeminus proper; V_{2g}, general cutaneous (+ communis) root of the trigeminus proper; V_{2m}, viscero-motor root of the n. trigeminus proper; VII, n. facialis; VIIe, electric roots or root of the n. facialis; VIIIa, anterior branch of the n. acusticus; VIIIp, posterior branch of the n. acusticus; IX, n. glossopharyngeus; X, n. vagus; X_{br1}—X_{br6}, branchial branches of the n. vagus.

perforatedat least in certain cases the cranial wall through the same canal (V, text-figs. 20—22; section series D, nos. 4—14) as the roots of the trigeminus proper.

Besides the root just described, the n. profundus presumably had a second rather fine root consisting of viscero-motor fibres. This root must have issued from the medulla oblongata somewhat antero-ventrally to the other root. In *Cephalaspis hoeli* it left the cavum cerebrale cranii through an independent canal, the canal V*a* (text-figs. 15—17; section series A, nos. 89—93; section series B, nos. 33—34), whereas in *Kiaeraspis* it may at least in certain cases have accompanied the root of the trigeminus proper and the general cutaneous root of the n. profundus through the canal V (text-figs. 21—22, section series D, nos. 4—14). It went to the myodome, which it reached somewhat medially to the other root of the same nerve. The n. profundus thus seems not to have consisted exclusively of general cutaneous and communis fibres but would appear in addition — contrary to what is the case in recent Cyclostomes and fishes — to have had a viscero-motor component. Accordingly it would in the Cephalaspids have been more complete than in other forms known so far, a condition which certainly must be considered as primitive.

The ganglion of the general cutaneous root of the n. profundus, which is referred to throughout this work as the profundus ganglion, certainly lay antero-dorso-medially to the ganglion gasseri and probably, like that, it was situated chiefly within the orbit, close to the myodome, though a medial part of it may have extended medially into the most dorso-latero-medial portion of the myodome.

After its origin from its ganglion the n. profundus passed forwards through the medial parts of the orbit not very high above the floor, but nevertheless certainly, in the usuall way, dorsally to the n. opticus. Close to the most anterior part of the orbit, thus after having traversed the orbit almost throughout its length, the n. profundus entered the canal V_1, (text-figs. 4, 13, 23, 24, 25, 27, 28, 36; section series A, nos. 120—155; section series B, nos. 43—55; section series C, nos. 72—88; section series D, nos. 1—20; pls. 13—15, 17—21, 27—29, 39, 44, 45, 48—51; pl. 54, fig. 1; pls. 55, 57, 58), from which it emerged into the antero-ventro-medial part of the oralo-branchial chamber, more exactly slightly hehind the ventral part of the prebranchial ridge in the anterior part of the first branchial fossa. At least in certain forms such as *Hoelaspis* (pl. 45) and *Kiaeraspis* (text-fig. 28; pls. 49, 50), it seems to have given off a branch to the dorso-medial parts of the oralo-branchial chamber, a branch which may have been nearest comparable to a r. visceralis, since the canal (V_{1v}) which transmitted it probably was a serial homologue to the canals through which the supposed visceral branches of the nn. glossopharyngeus, facialis and trigeminus proper went to the oralo-branchial chamber. If this conclusion is true, the n. profundus would thus also in this respect have been more complete and more in agreement with the ordinary branchial nerves than the corresponding nerves in the recent Cyclostomes and fishes.

Distally to the supposed visceral branch the n. profundus sent several branches to the neighbouring superficial parts of the shield; and, somewhat before it reached the oralo-branchial chamber, it broke up into an anterior branch, which took an antero-ventro-medial course towards the mouth, and one or more posterior branches, which probably went to the superficial parts of the shield, to the anterior half of the first branchial fossa and to the parts of the oralo-branchial chamber medially and anteriorly to that branchial fossa.

From its mode of branching at or just before its arrival into the oralo-branchial chamber, therefore, it is not difficult to conclude that the n. profundus probably supplied the mouth and the soft tissue in front of the first gill-sac, and since there probably was no well-developed velum it is very conceivable that it also innervated the most anterior visceral muscles. Its peripheral distribution thus forms a good support for the view advanced above that besides its other usual components — the general cutaneous and communis components — it also very well may be though to have had a viscero-motor component. Finally it should be added that probably, at least for a short distance within the orbit, it was accompanied by a fine nerve of lateralis fibres.

As far as we can judge, therefore, the n. profundus of the Cephalaspids was an independent branchial nerve, which had retained very primitive characters not found in the recent Cyclostomes and fishes. Expressed in another way: the n. profundus of the Cephalaspids had, more fully than that of other vertebrates, retained its primitive characters of an independent and complete branchial nerve.

The n. trochlearis issued from the brain in the ordinary way and went antero-laterally through the cavum cerebrale. It traversed the cranial wall in an antero-dorso-lateral direction through the canal IV (text-figs. 15—17, 20—23, 27; section series A, nos. 79—93;, section series B, nos. 31—38; section series C, nos. 29—48; section series D, nos. 23—39) and emerged into the orbit, more closely determined generally rather far postero-dorso-medially, a fact which perhaps suggests that the musculus obliquus superior was situated as in *Petromyzon* and not as in fishes. In *Cephalaspis hoeli* (text-figs. 15—17; section series A, nos. 79—93; section series C, nos. 29—48) and probably in all *Cephalaspis*-species and most other Cephalaspids too, the n. trochlearis, just when it entered its canal through the cranial wall on its way out from the cavum cerebrale cranii, crossed the general cutaneous root of the n. profundus on the dorsal side. And specially worthy of notice is that just at the crossing it was situated on the general cutaneous root of the n.

profundus. Its course and position in these forms were thus exactly as in the Petromyzontids (cf. AHLBORN 1883, pl. 13, fig. 2; 1884, pp. 298—299; CORNING 1900, p. 131; JOHNSTON 1902, pl. 1, fig. 1; pl. 8, fig. 30; 1905, pp. 177—178; KRAUSE 1923, fig. 430, p. 803). In *Kiaeraspis* (text-figs. 20—22, 27; section series D, nos. 23—39), on the other hand, it was, throughout its passage through the cranial wall to the orbit, situated rather far dorsally to the general cutaneous root of the n. profundus, but its relations to that root were probably nevertheless not different from what they were in the majority of forms, for it may very well be possible that it passed close above and crossed the said nerve root on the dorsal side already somewhat before its entrance into the cranial wall.

The n. oculomotorius always perforated the cranial wall rather close above the floor of the cavum cerebrale, slightly behind the dorsum sellae and the fenestra optica. It generally reached the orbit slightly behind the fenestra optica, or even at the very posterior border of that, rather far antero-ventrally to the n. trochlearis and somewhat anteriorly to the myodome; but in *Thyestes verrucosus* it seems to have emerged instead into the most antero-latero-medial part of the myodome. Its canal through the cranial wall is well seen in several specimens (III, text-figs. 15—17, 20—22, 28; section series A, nos. 96—100; section series C, nos. 31—36; section series D, nos. 10, 11, 13, 14; pl. 48, fig. 1; pls. 49, 55).

The n. opticus had its way out to the orbit through the big fenestra optica or, more correctly, through the dural membrane of connective tissue that closed that fenestra. As far as can be judged, it must have reached the orbit close above the bottom.

The n. olfactorius, which probably was paired, must have been very short. It certainly left the brain rather high above the floor of the cavum cerebrale cranii (text-fig. 32) and went straight forwards to the nasal capsule, after perforating the septum of connective tissue that separated this from the cavum cerebrale. As far as can be judged, it must in all respects have been as in the recent Cyclostomes (cf. text-figs. 32, 43).

Before we leave this chapter, it should be pointed out that the account given here of the cranial nerves is further elucidated by the restorations given in text-figs. 32 and 43.

Cranial vessels.

The heart was certainly situated close behind the basal part of the postbranchial wall. And in order to reach the oralo-branchial chamber, therefore, the truncus arteriosus had to pierce the postbranchial wall through the foramen *tr* (text-figs. 4, 36; pls. 15, 51, 52; pl. 53, figs. 2, 3;

pl. 58), or through the equivalent of this foramen in those cases when this was fused with the oesophagus foramen (text-figs. 33—35; section series C, nos. 12—69; section series F, nos. 25—59; pls. 9, 10; pl. 23, fig. 1; pl. 42; pl. 46, fig. 1; pl. 47, fig. 1). Well within the oralo-branchial chamber it went forwards, giving off afferent branchial arteries to the gill-sacs. And it is particularly noteworthy that anteriorly to the post-branchial wall it passed internally to the visceral endoskeleton and that this was the case also with all the afferent branchial arteries. Accordingly we find that the truncus arteriosus and the afferent branchial arteries in this respect were as in Petromyzontids.

After passing the gills the arterial blood was brought to the dorsal aorta through nine efferent branchial arteries and anteriorly to the first one of these, presumably through an artery which I have named the rostral artery (*a. rostz*, text-fig. 44), but which in fact was the efferent branchial artery of the premandibular visceral arch. Except the rostral artery, which carried the blood from the presumed anterior half of the prespiracular gill-sac, all the efferent branchial arteries arose from the adjacent halves of two neighbouring gill-sacs, quite as those in the Petromyzontids. And as in the Petromyzontids the rostral artery, as well as all the other efferent branchial arteries, passed internally to the visceral endoskeleton. In fishes, on the contrary, the efferent branchial arteries, as is well known, go entirely outside the branchial arches.

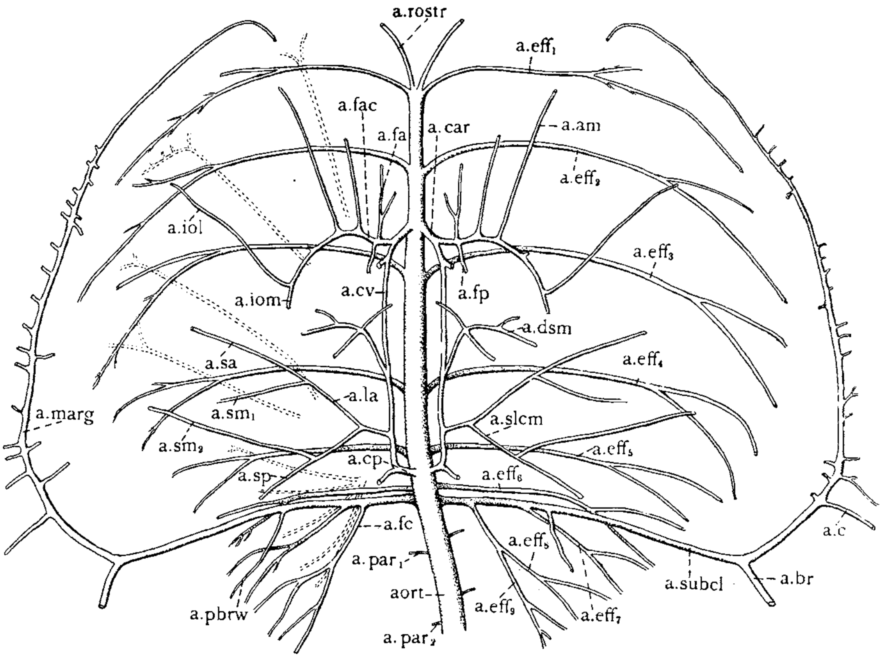
Passing over to details concerning the rostral artery and the efferent branchial arteries, we find the following.

The rostral artery (*a. rostr*) went in a postero-dorso-medial direction to the anterior end of the aorta and was throughout its extent situated entirely beneath the prebranchial ridge, which, at least in certain forms, is provided with a distinct groove for it (text-figs. 4, 36; pl. 51). To judge from its position, it seems very conceivable that it sent fine branches into the mucous membrane in the roof of the mouth. The three most anterior efferent branchial arteries (*a. eff*$_1$—*a. eff*$_3$, text-fig. 44), which had their passage close beneath the interbranchial ridges 1—3 respectively, and which in certain forms caused the formations of more or less distinct grooves on the dorso-medial parts of these ridges (text-figs. 4, 13, 36; pl. 44; pl. 46, fig. 1; pl. 51), also emptied directly into the aorta. The first of them arose from the adjacent halves of the prespiracular and spiracular gill-sacs, the second one from the adjacent halves of the spiracular and glossopharyngeal gill-sacs and the third one from the adjacent halves of the glossopharyngeal and first vagal gill-sacs.

The three efferent branchial arteries following next backwards — that is the efferent branchial arteries 4—6 (*a. eff*$_4$—*a. eff*$_6$, text-fig. 44) — took their origin from the gill-sacs in a corresponding way as the three in front and, like those they also passed dorso-medially beneath the interbranchial ridges corresponding to them (text-figs. 4, 33, 36). But while, as has been mentioned, the three in front all went directly to the aorta those under consideration here all opened into an unpaired short trunk, the arteria branchialis efferens communis (*a. eff. com*, text-figs. 39—41, 44, 45; section series F, nos. 7—26; pl. 46, fig. 1; pl. 47, fig. 1; pls. 51, 53, 58), which was situated within the most antero-dorso-medial part of the postbranchial wall, dorsally to the oesophagus foramen, and which opened anteriorly from the ventral side into the aorta. In this connection attention should be called to the fact that, at least in certain forms, a rather thick branch from the anterior half of the branchial sac 7 pierced the postbranchial wall and passed up to the a. subclavia. And it is thus highly probable that at least a rather considerable part of the arterial blood from the anterior half of the branchial sac 7 through this branch arrived in the a. subclavia and not in the efferent branchial artery 6.

Finally the most posterior efferent branchial arteries, the efferent branchial arteries 7—9 (*a. eff*$_7$—*a. eff*$_9$, text-figs. 4, 36, 39—41, 44; pl. 51), formed a group of their own, as none of the blood brought by them from the gill-sacs reached the aorta. The most anterior one of them that is to say the seventh one, — arose from the adjacent halves of the seventh and eight gill-sacs. Already after a rather short course within the oralo-branchial chamber, it left this and entered the postbranchial wall, in which it went antero-dorso-medially, emptying into the a. subclavia. The eighth one which carried blood from the adjacent halves of the eighth and ninth gill-sacs, and the ninth one, which, as has already been mentioned, drained the adjacent halves of the ninth and tenth gill-sacs, also both entered the postbranchial wall, within which they went antero-dorso-medially and soon joined each other. The common arterial trunk *a. fc* (text-figs. 36, 39, 40, 44), arisen by their junction, continued farther in an antero-dorso-medial direction and opened into the a. subclavia somewhat dorso-medially to the seventh efferent branchial artery.

The cephalic division of the dorsal aorta, that according to what has just been set forth, received its blood from the rostral artery, the efferent branchial arteries 1—3 and from the a. branchialis efferens communis, was a wide unpaired vessel (*aort*, text-figs. 44—46) which extented forwards even in front of the ethmoidal region, in fact even as far as a certain distance on to the internal surface of the rostral part of the visceral endoskeleton. And accordingly its extension forwards was much greater than in any other craniate vertebrate known in detail with regard to the arterial system, a condition which of course to a certain extent was due to the presence of the prespiracular and spiracular gill-sacs but which, however, must be chiefly explained as a result of the peculiar development of the rostral visceral parts of the head. Or expressed in another way: its unique forward extension, as being caused chiefly by the special development of the rostral visceral part of the head, was certainly a secondary feature. Just at its anterior end the cephalic division of the



Text-fig. 44. *Kiaeraspis*. Restoration of the chief arterial trunks with the exception of he truncus arteriosus, the afferent branchial arteries and other branches from the truncus arteriosus. The course of the branchial nerves shown in broken lines. $^7/_1$.

a. am, mandibular branch of the a. facialis; *a. br*, brachial artery; *a. c*, cornual artery; *a. car*, carotid artery; *a. cp*, occipital encephalic artery; *a. cv*, possible artery connecting the internal carotid and the posterior encephalic arteries; called in the description the arteria encephalica communicans; *a. dsm*, arteria superficialis postorbitalis; *a. eff*$_1$—*a. eff*$_9$, arteriae branchiales efferentes 1—9; *a. fa*, anterior branch from the a. facialis; *a. fac*, arteria facialis; *a. fc*, trunk arisen by the confluence of the efferent branchial arteries 8 and 9; *a. fp*, posterior branch from the a. facialis; *a. iol*, lateral infraorbital branch of the a. facialis; *a. iom*, medial infraorbital branch of the a. facialis; *a. la*, common trunk for the two anterior dorso-lateral superficial arteries; *a. marg*, arteria marginalis; *a. par*, first and second parietal arteries; *aort*, cephalic division of the aorta; *a. pbrw*, artery to the postbranchial wall; *a. rostr*, rostral artery; *a. subcl*, arteria subclavia; *a. sa*, *a. sm*$_1$, *a. sm*$_2$, *a. sp*, dorso-lateral superficial arteries 1—4; *a. slcm*, common trunk for the two posterior dorso-lateral superficial arteries.

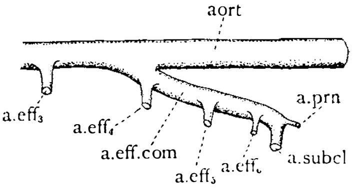
aorta received the rostral artery and, close behind that, the first efferent branchial artery. It passed straight backwards along the roof of the oralo-branchial chamber, leaving that chamber by perforating the most dorso-medial part of the postbranchial wall. During its passage through that wall it was thus enclosed in a short canal. Anteriorly and posteriorly to the postbranchial wall, on the contrary, it was situated only in a deep groove on the lower side of the endocranium, a groove (*aort. gr*) which is very distinctly seen in a number of specimens (text-figs. 2, 4, 13, 14, 36; section series A; section series B; section series D, nos. 1—10; pl. 23, fig. 3; pls. 28, 44; pl. 46, fig. 1; pl. 47; fig. 1; pl. 48, fig. 2; pls.

51—53; pl. 54, fig. 1; pl. 56, fig. 1; pls. 57, 58). While anteriorly to the posterior parts of the otic region it had a median position, it gradually left this during its passage through the postbranchial wall and turned to the right, so that finally, in the occipital region, it became situated entirely on the right side of the notochord and the neural ridge.

As far as can be judged from the conditions in the fossils, the branches given off from the cephalic division of the dorsal aorta were as follows: the carotid artery, the occipital encephalic artery and the parietal arteries. Among these we first deal with the carotid artery.

The carotid artery (*a. car*, text-fig. 44, 46; pls. 18—20, 22, 23, 28, 29, 42, 44, 45; pl. 46, fig. 1; pls. 51, 52; pl. 54, fig. 1; pl. 55, 57) was a paired vessel, which issued from the dorsal side of the cephalic division of the aorta somewhat in front of the efferent branchial artery 3 and beneath the transitional part between the ethmoidal and orbitotemporal regions. Diverging from its fellow of the opposite side it passed postero-dorso-laterally and penetrated into the ventral wall of the endocranium. In the *Cephalaspis*-species it went to the antero-lateral part of the fossa hypophyseos, where it divided into two branches, a medial one which was the internal carotid proper, and a lateral on which quite certainly was homologous with the a. facialis of the Petromyzontids (cf. text-fig. 99; cf. CORI 1906, pp. 33—34, pls. 5, 11,12; HATTA 1922, pp. 142—150; pl. 22), and which therefore is here called the a. facialis. In *Kiaeraspis* the carotid artery was apparently shorter than in the *Cephalaspis*-species, as it probably divided into the internal carotid proper and the a. facialis already during its passage through the ventral cranial wall.

Of the two chief branches of the carotid artery we shall first turn to the a. facialis. Immediately after its origin this artery *a. fac*, text-figs. 44, 46, 47, 49, 51) took first a dorsal and slightly antero-lateral direction. In those forms in which it left the carotid artery already before that artery had entered the cavum cerebrale cranii (*Kiaeraspis*) it went during this first part of its course entirely within the skeletal tissue situated antero-laterally to the cavum cerebrale, laterally to the ethmoidal cavity and medially to the anterior parts of the orbit. In those forms, on the contrary, in which it issued from the carotid artery just after that artery had entered the cavum cerebrale cranii (*Cephalaspis*), it had during the corresponding part of its course first to traverse a small antero-latero-ventral part of the cavum cerebrale before it could reach and perforate the skeletal tissue in front of that cavum, laterally to the ethmoidal cavity and medially to the anterior parts of the orbit. During the ascendent part of its course now in question it gave off several fine branches to the anterior part of the cavum cerebrale cranii and to the ethmoidal cavity. After arriving rather close beneath the dorsal surface of the ethmoidal region, in the angle between the orbit and the ethmoidal cavity, it suddenly turned laterally or latero-posteriorly, and just at the point at which it thus changed its



Text-fig. 45. Sketch showing the position and relations of the arteria branchialis efferens communis in a Cephalaspid. *aort*, cephalic division of the aorta; *a. eff*$_3$— *a. eff*$_6$, arteriae branchiales efferentes 3—6; *a. eff. com.* arteria branchialis efferens communis; *a. prn*, arterial branch to the pronephros space; *a. subcl*, arteria subclavia.

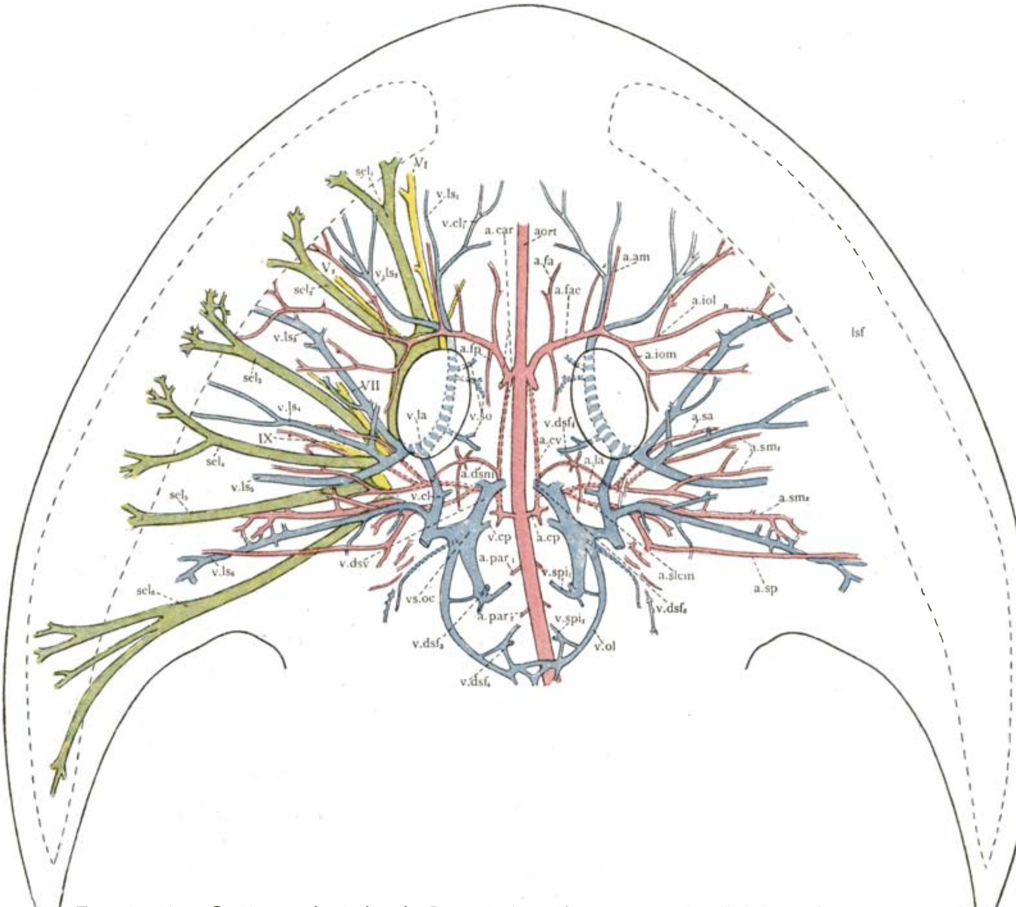
course it regularly gave off two rather strong branches, an anterior and a posterior one.

The anterior one (*a. fa*, text-figs. 28,44, 46, 47, 51 pls. 27, 28, 49, 55) of these two branches passed forwards somewhat laterally to the nasal aperture, gradually ascending to the dorsal surface of the ethmoidal region, on which it soon broke up into very numerous branches. How far forwards it really did reach it is difficult to decide exactly; but there can be no doubt that certain of its branches went at least as far as until somewhat antero-laterally to the nasal aperture and accordingly so far forwards that they carried blood to the dorsal field of the external surface of the rostral part of the visceral endoskeleton. The posterior branch (*a. fp*, text-figs. 28, 44, 46, 47, 49), on the other hand, went to the bottom of the fossa circumnasalis and the upper surface of the prepineal part of the interorbital wall. Like the anterior one, it branched abundantly (cf. pl. 39).

At least in certain cases, other branches with a finer calibre issued from the arteria facialis at the point were it changed its course from a chiefly dorsal to a chiefly lateral one — branches which went to the division of the ethmoidal cavity for the hypophyseal sac and to the upper surface of the ethmoidal region.

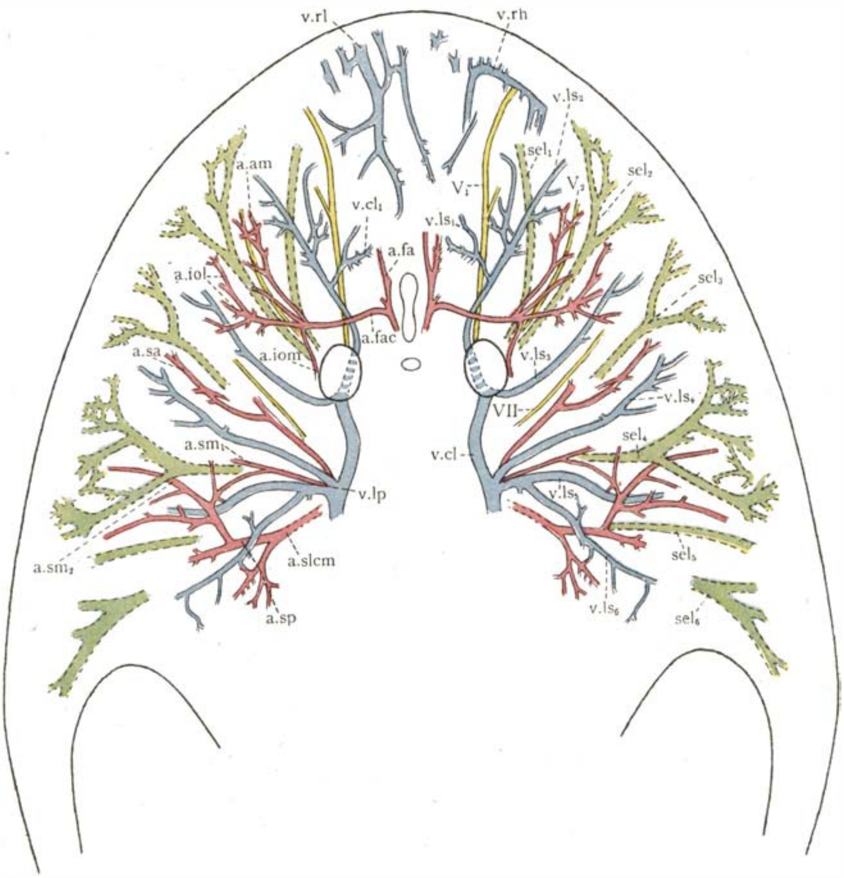
After having turned laterally and after having given off the branches described, the arteria facialis soon arrived at the dorsal surface of the ethmoidal region, on which it then passed laterally — or in several forms, postero-laterally — more or less close in front of the anterior end of the orbital opening. During this part of its course it gave off a rather strong superficial branch in an anterior direction (text-fig. 44), a branch which was situated antero-medially to the n. profundus, and which therefore will be called the premandibular branch (*a. am*, text-fig. 46).

Somewhat antero-laterally to the orbital opening and distally to the premandibular branch the arteria facialis generally divided into three main superficial branches. The most posterior one of these three branches, the medial infraorbital branch (*a. iom*, text-figs. 28, 44, 46—49, 51; pls. 27, 29, 30, 39), went posteriorly more or less close to the ventral (external) margin of the orbital opening, sending out numerous branches, especially on its lateral side. It seems to have reached as far backwards as the posterior end of the orbital opening. The branch next in front of the one just described went postero-latero-ventrally to the dorsal field of the external surface of the lateral part of the visceral endoskeleton, on



Text-fig. 46. *Cephalaspis heintzi*. Restoration of the cephalic division of the aorta and the chief superficial vessels of the dorsal side of the cephalic shield (save the rostral and marginal ones). Certain of the nerves also drawn. Arteries red, veins blue, electric nerves green, ordinary nerves yellow. The restoration is based chiefly on the specimen figured in pls. 29 and 30.

a. am, premandibular branch of the a. facialis (mandibular branch not lettered); *a. car*, carotid artery; *a. cp*, occipital encephalic artery; *a. cv*, possible artery connecting the carotid and the posterior encephalic arteries called in the description the arteria encephalica communicans; *a. dsm*, arteria superficialis postorbitalis; *a. fa*, anterior branch from the a. facialis; *a. fac*, arteria facialis; *a. fp*, posterior branch from the a. facialis; *a. iol*, lateral infraorbital branch of the a. facialis; *a. iom*, medial infraorbital branch of the a. facialis; *a. la*, arterial trunk which divided into the two anterior dorso-lateral superficial arteries; *a. par*$_1$, *a. par*$_2$, parietal arteries 1 and 2; *aort*, cephalic division of the aorta; *a. sa*, *a. sm*$_1$, *a. sm*$_2$, *a. sp*, dorso-lateral superficial arteries 1—4; *a. slcm*, common trunk for the two posterior dorso-lateral superficial arteries; *lsf*, lateral electric field; *sel*$_1$—*sel*$_6$, nerves for the lateral electric field; *v. cl*, vena capitis lateralis; *v. cl*$_1$, preorbital part of the v. capitis lateralis; *v. cp*, v. cerebralis posterior; *v. dsf*$_1$—*v. dsf*$_4$, veins from the dorsal electric field; *v. dsv*, otical vein; *v. ls*$_1$—*v. ls*$_6$, dorso-lateral superficial veins 1—6; *v. ol*, lateral occipital vein; *vs. oc*, occipital vein sinus; *v.so*, supraorbital veins; *v. spi*$_1$, *v. spi*$_2$, myelonal veins 1, 2; V_1, n. profundus; V_{1v}, visceral ramus of the n. profundus; V_2, n. trigeminus proper; *VII*, n. facialis; *IX*, n. glossopharyngeus.



Text-fig. 47. *Cephalaspis vogti.* The chief superficial vessels of the dorsal side of the cephalic shield. The electric nerves for the lateral electric field green. The cranial nerves yellow. Arteries red, veins blue. Chiefly after the specimen figured in pl. 27. Magnification about $^3/_1$.

a. am, mandibular branch of the a. facialis; *a. fa*, anterior branch from the a facialis; *a. fac*, arteria facialis; *a. iol*, lateral infraorbital branch of the a. facialis; *a. iom*, medial infraorbital branch of the a. facialis; *a. sa*, *a.* sm_1, *a.* sm_2, *a. sp*, dorso-lateral superficial arteries 1—4; *a. slcm*, common trunk for the two posterior dorso-lateral superficial arteries; sel_1—sel_6, nerves for the lateral electric field; *v. cl*, vena capitis lateralis; *v.* cl_1, preorbital portion of the vena capitis lateralis; *v. lp*, venous trunk arisen by the confluence of the three posterior dorso-lateral superficial veins; *v. rh*, *v. rl*, rostral veins, asymmetrically developed; *v.* ls_1—*v.* ls_6, dorso-lateral superficial veins 1—6; V_1, n. profundus; V_2, n. trigeminus proper; VII, n. facialis.

which it continued with its terminal ramifications down into the lateral electric field. More exactly determined this branch, which will be termed the lateral infraorbital branch (*a. iol*, text-figs. 28, 44, 46, 47, 49, 51; pls. 27, 29, 30, 39), passed on the portion of the visceral endoskeleton situated between the n. facialis and the n. trigeminus proper, and on account of this fact it could also be properly called the hyoid branch. Finally the third and most anterior of the three branches in question (*a. am*, text-figs. 28, 44, 46 (in this figure it is not denoted by any letters), 47, 49; pls. 27, 29, 30, 39) always passed off antero-latero-ventrally on the upper surface of the portion of the lateral part of the visceral endoskeleton situated between the n. trigeminus proper and the n. profundus. Like the lateral infraorbital branch, it supplied most distally a portion of the lateral electric field. On account of its position it will be called the mandibular branch.

From what has been said, therefore, we find that the arteria-facialis supplied certain anterior parts of the cavum cerebrale, the ethmoidal cavity, the fossa circumnasalis and the posterior superficial parts of the ethmoidal region in general, further certain anterior and antero-lateral superficial parts of the orbitotemporal region and finally certain anterior and lateral superficial parts of the visceral endoskeleton.

The internal carotid proper, if we now turn to that, soon broke up into several branches within the cavum cerebrale cranii. One of these branches was the arteria ophthalmica magna, which, probably more or less closely associated with the n. opticus, emerged into the orbit after perforating the membrane of connective tissue which closed the fenestra optica. Other branches of the internal carotid artery proper supplied the brain, and finally one branch of that artery probably passed backwards along the floor of the cavum cerebrale and joined a branch from the occipital encephalic artery. Accordingly, if I am right, there would thus have been a communication between the carotid artery and the occipital encephalic artery, a communication (*a. cv*, text-figs. 44, 46) which at least partly might have corresponded to the vessel in *Petromyzon* called by CORI (1906, pp. 35—36) the ramus posterior of the carotis and by HATTA (1922, pp. 145—146) the posterior cerebral artery. We shall here employ for it the term of a. encephalica communicans.

Opposite the most anterior ventral part of the medulla oblongata the a. encephalica communicans probably gave off a rather strong branch (*a. dsm*, text-figs. 15, 17, 20, 22, 23, 27, 44, 46, 49), which, after traversing the cavum cerebrale in a dorsal direction, entered the dorsal wall of the endocranium just antero-dorsally to the cerebellum. More closely defined, this branch after it had left the cavum cerebrale cranii perforated the portion of the dorsal wall of the endocranium situated between the cavum cerebrale cranii medially, the orbit antero-laterally and the canalis semicircularis anterior postero-laterally. In virtue of its position, therefore, it may properly be called the a. superficialis postorbitalis. Somewhat beneath the dorsal surface of the endocranium it divided into several branches which diverged from each other and carried blood to the postero-dorso-medial part of the upper surface of the orbitotemporal region, to the anterior and middle parts of the upper surface of the otic region, and to the anterior half of the dorsal electric field.

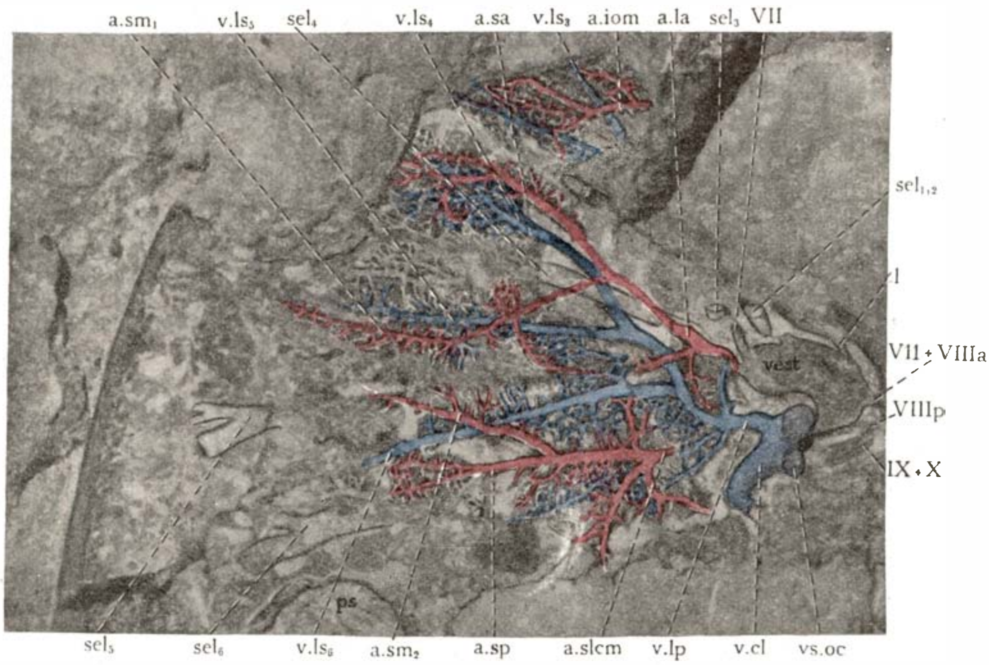
The occipital encephalic artery (*a. cp*, text-figs. 16, 21, 24, 44, 46) issued from the cephalic division of the dorsal aorta close before or just after this had perforated the post-branchial wall. Immediately after its origin, which was on the dorsal side of the cephalic division of the dorsal aorta, it took a dorsal or slightly dorso-lateral direction, perforated the ventral wall of the neurocranium and entered the cavum cerebrale cranii somewhat medially — or, in certain cases, perhaps slightly antero-medially — to the internal opening of the vagus canal. Well within the cavum cerebrale cranii it probably soon broke up into several branches, one of which, as has already been pointed out, probably may have joined a posterior branch from the carotid artery in order to form with this the presumed arteria encephalica communicans, while others supplied the posterior parts of the brain and the posterior parts of the cavum cerebrale cranii. Attention should also be called here to the fact that the occipital encephalic artery of the right side usually was situated somewhat in front of that of the left side (not well shown by text-figs. 45 and 46).

From one of the arteries in the cavum cerebrale, probably the a. encephalica communicans, a rather strong branch must have issued in a lateral direction to the vestibular division of the labyrinth cavity. How this branch, which we may call the otico-superficial artery, reached the said division of the labyrinth cavity, and how it went within that division, cannot be made out with certainty. What is seen of it in text-figs. 44, 46 and 49 is therefore only to be considered as an attempted restoration, with the chief object of giving an approximate idea of its general relations. During its passage through the vestibular division of the labyrinth cavity the otico-superficial artery probably supplied certain parts of the membranous labyrinth and adjacent portions of the walls of the labyrinth cavity, after which it generally broke up into four chief lateral branches, which all penetrated into the lateral wall of the labyrinth cavity. From that wall, and thus from the most lateral portion of the otic region, these branches, which will be termed the dorso-lateral superficial arteries (*a. sa*, *a.* sm_1, *a.* sm_2, *a. sp*, text-figs. 44, 46—49; in several of the plates 17—30, and pls. 39, 49, 50 and 55), arrived to the dorsal field of the external surface of the lateral part of the visceral endoskeleton, on which they branched very abundantly. With their most distal rami they reached down to and supplied the posterior parts of the lateral electric field.

The dorso-lateral superficial arteries were either independent of each other throughout their extent, and thus already from their origin in the vestibular division of the labyrinth cavity, or else they united with each other in different ways for a short distance just laterally to the labyrinth cavity and thus in the most lateral part of the otic region. In most cases we find (text-figs. 44, 46—49) that this union took place in such a way that of the arteries in question the second one ($a.sm_1$) had moved somewhat forwards and fused for a short stretch with the first one (*a. sa*) into a common trunk (*a. la*), and that, in a similar way, the third one (*a.* sm_2) had shifted backwards and for a short stretch joined the fourth one (*a. sp*) and formed a likewise short common trunk (*a. slcm*). In other cases it is clearly seen that the two posterior of these arteries were quite independent throughout their extent, whereas the two anterior ones had fused with each other for a short stretch laterally to the labyrinth cavity. The most anterior dorso-lateral superficial artery or, in those cases when this was united with the one next behind, the short trunk arisen by the union of these two arteries left the vestibular division of the labyrinth cavity close behind the n. facialis and sometimes even through the same canal as that nerve, though it always rather soon entered a canal of its own. All the arteries in question emerged from the vestibular division of the labyrinth cavity dorsally to the electric nerves for the lateral electric field, the two most anterior ones approximately above the fourth and fifth of these nerves, the two posterior ones approximately above the interspace between the fifth and sixth or above and slightly posteriorly to the sixth of the same electric nerves. Concerning their position laterally to the otic region it should further be noticed here that of the dorso-lateral superficial arteries the first one (*a. sa*) passed above the portion of the visceral endoskeleton between the n. facialis and the n. glossopharyngeus, that the second and third ones (*a.* sm_1, *a.* sm_2) went on the portion of the visceral endoskeleton falling between the n. glossopharyngeus and the first branchial branch of the n. vagus, and that the fourth and most posterior one (*a. sp*) had its passage on the portion of the visceral endoskeleton behind the first branchial branch of the n. vagus. And we are thus able to establish the fact that they alternated in a certain regular way with the branchial nerves, a fact which indicates that, like the superficial branches of the a. facialis, they had a distinctly metameric disposition. Accordingly the entire arterial system of the dorsal field of the external surface of the rostral and lateral parts of the visceral endoskeleton was metamerically arranged.

In this connection it should further be mentioned that a rather strong branch regularly issued in a postero-lateral direction either from the proximal part of the dorso-lateral superficial artery 4 or, if this was united with the one next in front, from the common trunk formed by the union of these two arteries. This posterior branch, which is well shown in text-figs. 47, 48, has such a position that it seems to have represented either a seventh dorso-lateral-superficial artery or such an artery together with a number of still more posterior though vestigal dorso-lateral superficial arteries, accordingly vestigal dorso-lateral superficial arteries belonging to the parts of the visceral skeleton behind the second branchial branch of the n. vagus.

Besides the postorbital and otico-superficial arteries there arose also, from the encephalic arteries, a couple of fine arterial branches for



Text-fig. 48. *Cephalaspis vogti.* Part of the system of canals particularly for superficial vessels on the dorsal side of the cephalic shield. Canals for arteries red; canals for veins blue. Same specimen as that figured in pl. 25. Somewhat magnified.

a. iom, canal for the medial infraorbital branch of the a. facialis; *a. la*, canal for an arterial trunk arisen by the union of the canals for the dorso-lateral superficial arteries 1 and 2; *a. sa*, canal for the dorso-lateral superficial artery 1; *a. slcm.* canal for an arterial trunk arisen by the union of the canals for the dorso-lateral superficial arteries 3 and 4; $a.\,sm_1$, $a.\,sm_2$, *a. sp*, canals for the dorso-lateral superficial arteries 2—4; *l*, canal for the lateralis fibres, that went to the orbit; *ps*, pectoral sinus; $sel_{1,\,2}$, common canal for the two most anterior nerves for the lateral electric field; sel_3—sel_6, canals of the nerves 3—6 for the lateral electric field; *v. cl*, canal for the v. capitis lateralis; *vest*, vestibular division of the labyrinth cavity; *v. lp*, common canal for the posterior three dorso-lateral superficial veins; $v.\,ls_3$—$v.\,ls_6$, dorso-lateral superficial veins 3—6; *vs. oc*, occipital vein sinus; VII, canal for the passage of the n. facialis to the oralo-branchial chamber; VII + VIII *a*, acustico-facialis canal; for the roots of the n. facialis proper, for the electric nerve fibres, for the prootic lateralis fibres and for the anterior branch of the n. acusticus; VIII*p*, canal for the posterior branch of the n. acusticus; IX+X, vagus canal, for the glossopharyngeus and vagus, and for the v. cerebralis posterior.

the dorsal surface of the most anterior part of the interorbital wall, i. e. the antero-dorso-medial part of the upper surface of the orbito-temporal region. These arteries traversed the canals ax_1 and ax_2 (text-figs. 20, 22, 27; section series B, nos. 36—38; section series D, nos. 25—43).

In this connection it should also be noticed that a branch from the encephalic system of arteries perhaps ascended to the dorsal parts of the labyrinth region through the canal *dx* (text-figs. 15, 17, 20, 22, 26; section series A, nos. 49—52; section series C, nos. 1—7, 26—30; section series D, nos. 14—23).

Of the branches which were given off by the cephalic division of the dorsal aorta the parietal arteries still remain to be dealt with. These arteries were in the *Cephalaspis*-species generally 2—3 (*a. par*$_1$, *a. par*$_2$, etc. text-fig. 46), while in *Kiaeraspis* and other forms with a long occipital region they certainly were much more numerous. As in the case of the spino-occipital nerves, those of the right and left sides certainly alternated with each other in such a way that each one of those of the right side was always situated somewat in front of the corresponding one of those of the left side. During their passage upwards they certainly gave off the myelonal arteries to the most posterior portion of the cavum cerebrale cranii through the canals for the ventral roots of the spino-occipital nerves.

From the arteria branchialis efferens communis there issued, as has already been mentioned, most posteriorly the paired strong arteria subclavia (*a. subcl*, text-figs. 36, 44, 45) which was lodged in the canal lettered *a. subcl* in the figures (text-figs. 9—12, 34, 36, 39, 40, 44, 45, 52; section series F, nos. 11—48; pls. 20, 22, 28; pl. 46, fig. 1; pl. 47, fig. 1; pls. 51—53, 58). More exactly, the arteria subclavia passed off from the arteria branchialis efferens communis within the postbranchial wall above the medial end of the interbranchial ridge 6. During its further course it went first for a rather considerable stretch above the interbranchial ridge 6 either in a straight lateral or in a lateral and slightly ventral direction and received here the efferent branchial arteries 7—9 in the way described above (cf. text-figs. 36, 39, 40, 44). Somewhat laterally to the point at which the efferent branchial artery 7 opened into it, it always turned somewhat postero-ventrally, so that it entered and pierced the latero-ventral part of the half of the postbranchial wall of its side, after which it reached the basal part of the endoskeletal shoulder-girdle. Soon after its entrance into the endoskeletal shoulder-girdle it gave off a very strong branch in a postero-lateral direction to the pectoral sinus, a branch which carried blood to the pectoral fin and which therefore will be called the arteria brachialis (*a. br*, text-figs. 12, 36, 39, 40, 44). On the stretch between this artery and the efferent branchial artery 7 or slightly distally to that the arteria subclavia sent a branch to the posterior surface of the postbranchial wall (*a. pbrw*, text-fig. 44).

Beyond the point at which the arteria brachialis issued from it the arteria subclavia continued in a lateral direction through the basal part of the endoskeletal shoulder-girdle and gave off a ventral branch which went down to the lower side of the endoskeletal shoulder-girdle and the adjacent portion of the ventral field of the lateral part of the visceral endoskeleton. This branch, which was a superficial branch, will be termed the ramus superficialis ventralis of the arteria subclavia. On account of its ventral position the canal which transmitted it is rarely to be observed (*a. vs*, text-fig. 40; section series F, nos. 42—60).

From the basal part of the endoskeletal shoulder-girdle the a. subclavia entered the proximal part of the cornu of its side, within which it immediately divided into two thick branches, an antero-lateral one, and a postero-lateral one.

The former of these two branches (*a. marg.* text-fig. 44) first traversed the most proximal anterior part of the cornu in an antero-lateral direction. Then it curved more forwards and, during the rest of its course, went forwards close along the lateral margin of the shield within the most latero-ventral part of the visceral endoskeleton coalesced with the endocranium. Because of this marginal course it has been called here the arteria marginalis. During the greater part of its course it was lodged in a canal of its own, the one lettered *a. marg*, in the figures (text-figs. 12, 36, 39; section series 156—158; section series F, nos. 35—65; pls. 20, 22, 44, 51), but anteriorly to that canal it presumably traversed the most anterior portion of the canal *v. marg*, from which it probably entered the canal *v. a*, (text-figs. 36; pl. 51). Within the latter canal it may have passed over into an anterior narrow branch from the truncus arteriosus, a branch which, if it went as I imagine, must have entered the canal *v. a*, through the anterior opening. If this was so — and at present I can find no better explanation for the function of the canal *v. a*, than the one just given — it would of course imply that the anterior part of the marginal artery contained a mixture of oxydized and unoxydized blood. The marginal artery gave off numerous branches in medial, lateral, latero-ventral and ventral directions, all of which, except, the medial ones, which went to the interior of the lateral parts of the shield, ended beneath and within the exoskeleton. The majority of these branches were thus superficial ones and the a. marginalis was consequently, in the main, a superficial vessel.

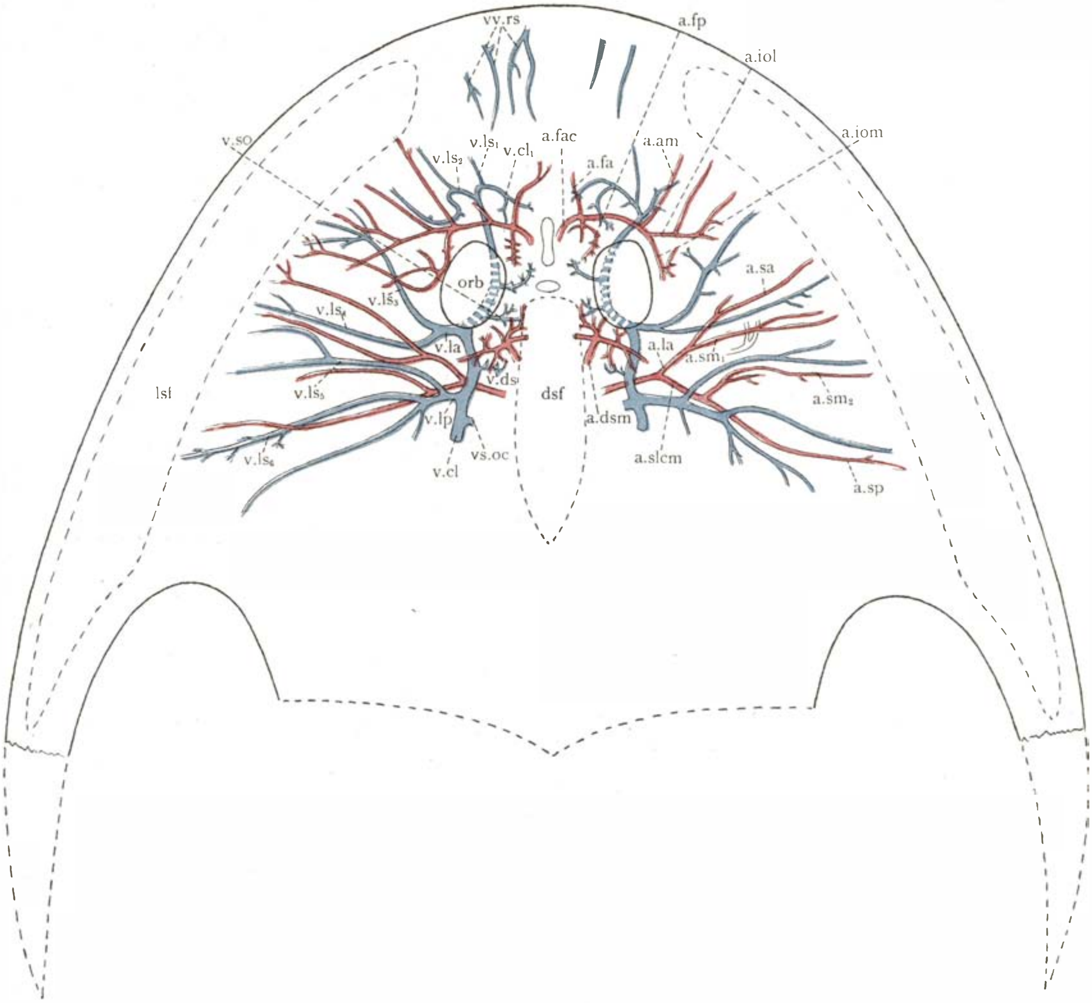
The other branch arisen by the subdivision of the arteria subclavia (*a. c*, text-figs. 39, 44) went postero-laterally within the cornu and on account of this it will be called the arteria cornualis. It branched abundantly and at least the majority of its branches were superficial ones. In the forms with a small cornu it was rather small, whereas in the forms with a well developed cornu it attained a considerable size. The canal for it is partly shown in a few specimens (text-figs. 12, 33, 36, 39, 40, 52 section series A, nos. 159—162, section series F, nos. 34—55; pl. 39).

As we find from the facts now given concerning it, the a. subclavia and its branches carried blood to the postbranchial wall, to the pectoral fin, and the shoulder-girdle, to the cornu and to the most latero-ventral parts of the shield almost as far forwards as the rostrum. Of its branches the marginal artery, the cornual artery and the ramus superficialis ventralis were chiefly or entirely superficial.

Because of the fact that the arteriae branchiales efferentes 7—9 opened into the a. subclavia, it is highly probable that the part of this artery situated medially to the efferent branchial artery 7 had arisen by the union of the three hindmost efferent branchial arteries. In reality, therefore, this part should perhaps not be included in the a. subclavia, but for the sake of simplicity this has, however, been done here. In all the figures it has also been denoted as belonging to the a. subclavia.

From what has been set forth here concerning it we find that the arteria subclavia arose in relation to the posterior efferent branchial arteries, and that both in this and in other respects it presented such considerable agreements with the similarly named artery of fishes that, as far as can be judged, it must have been homologous with that (cf. AYERS 1889, figs. 1, 10; DANIEL, 1922, pp. 173—174, 197—199, figs. 148, 153, 157, 158, 162, 169; PARKER, T. J., 1887, pp. 696—697, pl. 34, figs. 1, 2; pl. 35, fig. 6; ALLEN, 1905, pp. 46, 63, 64, 115). The marginal artery was in certain respects suggestive of the artery of fishes described by DANIEL (1922, p. 168) and others (PARKER, T. J., 1887, etc.) as the coracoid artery and by ALLEN (1905, pp. 49—50, 115, etc.) as the hypobranchial artery, but as it went dorsally to the branchial openings, it cannot of course have been homologous with that artery.

The superficial arteries — thus the facial artery, the postorbital superficial artery, the dorso-lateral superficial arteries, the marginal artery, the cornual artery and the ramus superficialis ventralis of the subclavian artery — after having arrived at the respective external surfaces of the endoskeleton, broke up into numerous branches, which in their turn divided abundantly into very fine twigs which anastomozed with each other so that a vascular plexus was formed between the exoskeleton and the endoskeleton. This plexus which — beause of this position will be referred to throughout this work as the subaponeurotic vascular plexus — is, as we have already found (cf. pp. 34, 35 above), in fact situated in part on the external surfaces of the endoskeleton, in part within the most basal portion of the basal layer of the exoskeleton. Since, however, we have reason to believe that the most basal portion of the basal layer of the exoskeletal bone is not of dermal origin, but instead presumably represents the perichondral — respectively the periostal (bone) layer of the endoskeleton (cf. pp. 40—41 above), the subaponeurotic vascular plexus would thus in reality have been situated just beneath the exoskeleton. The canals of the subaponeurotic vascular plexus are in part well displayed in surface view in pls. 25 and 39 and in section in pl. 64, fig. 2, pls. 65, 66 (*dplx*).



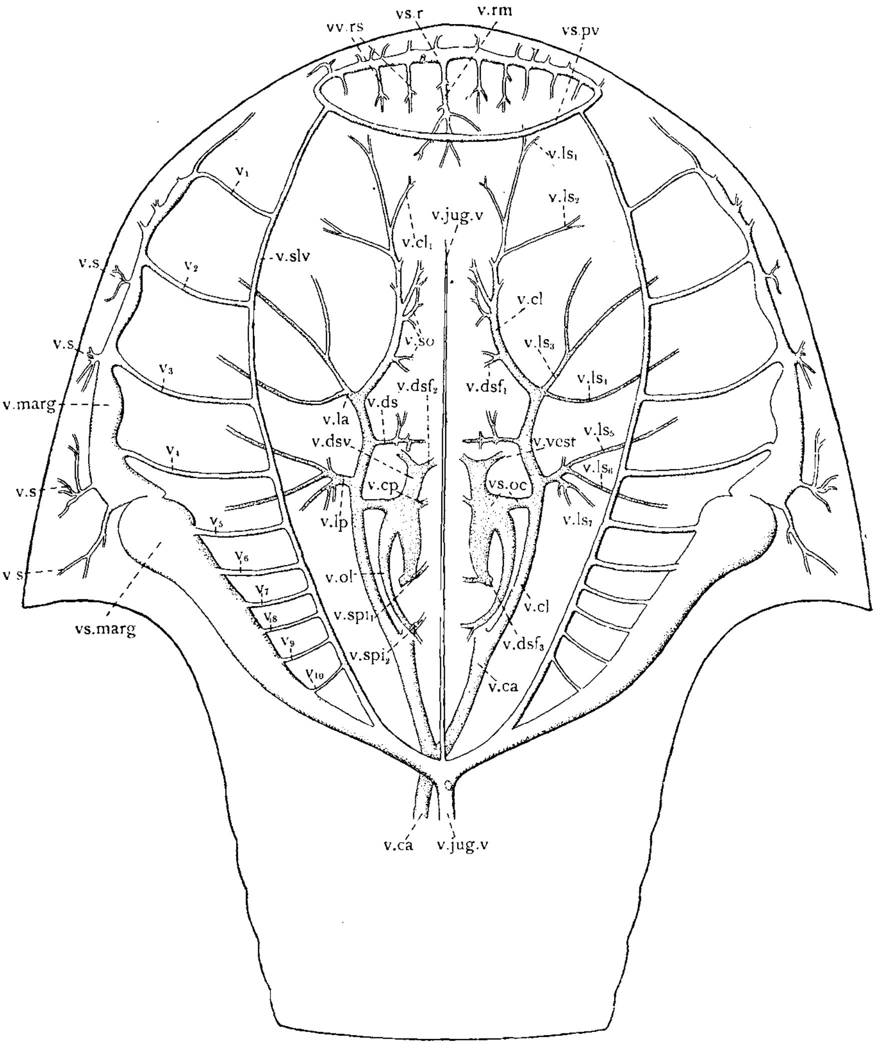
Text-fig. 49. *Cephalaspis spitsbergensis*. Restoration of the chief superficial vessels of the dorsal side of the endoskeletal component of the cephalic shield. The restoration made chiefly after the specimen figured in pl. 39. Arteries red, veins blue. Magnified.

a. am, mandibular branch of the a. facialis; *a. dsm*, arteria superficialis postorbitalis; *a. fa*, anterior branch from the a. facialis; *a. fac*, arteria facialis; *a. fp*, posterior branch from the a. facialis; *a. iol*, lateral infraorbital branch of the a. facialis; *a. iom*, medial infraorbital branch of the a. facialis; *a. la*, common trunk for the dorso-lateral-superficial arteries 1 and 2; *a. sa*, *a. sm*$_1$, *a. sm*$_2$, *a. sp*, dorso-lateral superficial arteries 1—4; *a. slcm*, common trunk for the dorso-lateral superficial arteries 3 and 4; *dsf*, dorsal electric field; *lsf*, lateral electric field; *orb*, orbit; *v. cl*, vena capitis lateralis; *v. cl*$_1$, preorbital part of the v. capitis lateralis; *v. ds*, dorsal vein from the part of the cranial roof above and between the semicircular canals; *v. la*, common trunk for the dorso-lateral superficial veins 3 and 4; *v. lp*, common trunk for the dorso-lateral superficial veins 5 and 6; *v. ls*$_1$—*v. ls*$_6$, dorso-lateral superficial veins 1—6; *vv. rs*, rostral superficial veins; *v. so*, supraorbital veins; *vs. oc*, occipital vein sinus (only the part of it which opened into v. capitis lateralis to be seen.

The subaponeurotic vascular plexus gave off branches in an external direction, branches which traversed the ascending canals (*c. asc*, pl. 64, fig. 2; pl. 65, fig. 2; pl. 66; pl. 67, fig. 1) through the basal layer of the exoskeleton and penetrated into the middle layer of that, in which they branched very abundantly and formed a vascular plexus. This vascular plexus, which was thus situated within the middle layer of the exoskeleton, has already been described above (pp. 35, 36) as the subepidermal vascular plexus. In the basal parts this plexus consisted of vessels, which, as we have found, radiated from the centre or the central parts of each polygonal area and passed over into the radiating vessels of the adjacent polygonal areas. The canals (*rad.c*) which lodged these radiating vessels are clearly shown in pls. 64—67, and 69 and 70. On the external side the radiating vessels gave off several fine twigs outwards, which in their turn branched and anastomozed with each other. The canals for these external twigs (*ebc*), which are difficult to study with regard to details, are shown in section in pls. 64, 65; pl. 66, fig. 1 and pl. 67.

From the subepidermal vascular plexus a great number of minute veins arose, veins which united with each other and formed thicker veins. All these veins were situated between the exoskeleton and the endoskeleton and thus they were all superficial veins. As is shown by text-figs. 46—49 they were not — with the exception of the finest ones — situated quite as superficially as the superficial arteries, but slightly beneath these. On the dorsal and lateral sides of the endoskeleton (the upper side of the cephalic shield) they may, according to their disposition and mode of emptying into the deeper veins, be divided into four groups which were as follows: a rostral group, a ventrolateral group, a dorso-lateral group and a dorso-medial group. All, these groups, except the rostral one, were paired.

The rostral group, if we first consider that, drained a more or less considerable anterior part of the dorsal (external) surface of the rostral part of the visceral endoskeleton, and it always emptied into a rather wide transversal sinus in the rostral margin of the shield, a sinus (*vs. r*, text-fig. 50) which may be termed the rostral vein sinus. As will be shown more in detail below in the account of the dorso-lateral group it was often asymmetrically developed. In its simplest original conditions it probably consisted of numerous rather fine and short veins, the rostral veins, which went forwards and downwards to the rostral vein sinus independently of each other. In none of the forms known so far, however, it has been found in such a condition, but a more or less great number of its veins had always united with each other to form larger trunks which poured out into the rostral vein sinus. In certain forms, such as *Kiaeraspis* (text-fig. 50), only a few of the medial rostral veins had united with each other into an unpaired rather large median rostral vein



Text-fig. 50. *Kiaeraspis auchenaspidoides.* Attempted restoration of the chief trunks of the venous system. Ventral aspect. Magnification about $^7/_1$.

v. ca, anterior cardinal vein; *v. cl*, vena capitis lateralis; *v. cl*$_1$, preorbital portion of the vena capitis lateralis; *v. cp*, vena cerebralis posterior; *v. ds*, dorsal chiefly superficial vein branch from the dorso-lateral parts of the otic region (the angle between the two semicircular canals. *v. dsf*$_1$– *v. dsf*$_3$, anterior middle and posterior veins from the dorsal electric field; *v. jug. v*, vena jugularis ventralis; *v. la*, common trunk formed by the union of the dorso-lateral superficial veins *v. ls*$_3$ and *v. ls*$_4$; *v. lp*, common trunk formed by the union of the dorso-lateral superficial veins *v. ls*$_5$ and *v. ls*$_6$; *v. ls*$_1$—*v. ls*$_7$, dorso-lateral superfictal veins 1—7; *v. marg*, marginal vein; *v. ol*, lateral occipital vein; *v. rm*, median rostral vein, arisen by the union of a few medial rostral veins; *v. s*, superficial veins which emptied into the marginal vein; *v. so*, supraorbital veins; *vs. marg*, posterior division of the marginal vein; *vs. oc*, occipital vein sinus; *v. slv*, vena superficialis longitudinalis ventralis; *v. spi*$_1$, *v. spi*$_2$, myelonal veins 1, 2; *vs. pv*, vein sinus which together with the rostral vein sinus formed an annular vein sinus around the mouth opening; *vs. r*, rostral vein sinus; *vv. rs*, rostral superficial veins; *v. vest*, vein from the vestibular division of the labyrinth cavity; *v*$_1$—*v*$_{10}$, ventral transversal superficial veins.

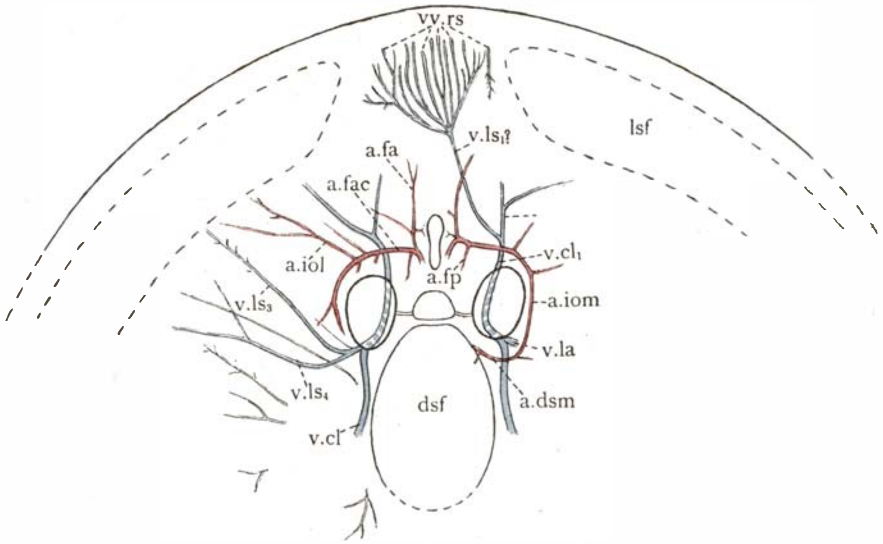
(*v. rm*), while the lateral rostral veins of each side retained their independence. In other forms, such as *Cephalaspis spitsbergensis* (text-fig. 49) only a few of the lateral rostral veins met and united with each other. Finally in *Cephalaspis vogti* (text-fig. 47) the rostral veins on each side of the median line had almost all joined into a common trunk, but while this trunk on the left side (*v. rl*) was situated chiefly longitudinally and had a rather considerable extension backwards it was, on the contrary, on the right side (*v. rh*) almost transversal and drained an area which reached less far backwards than on the left side. We thus find that great variations occurred with regard to the disposition and extension of the rostral group of superficial veins not only in different genera but also in different species of the same genus. It also seems probable that the rostral group of superficial veins varied much in different specimens of the same species; but the material available did not enable me to undertake any detailed studies of this.

The ventro-lateral group of dorsal superficial veins drained the parts of the visceral skeleton of the cephalic shield situated laterally to and beneath the lateral electric field, that is, the dorsal portion of the most ventral part of the visceral skeleton coalesced with the endocranium. In addition it probably carried blood also from the most lateral part of the lateral electric field. It consisted of short, mostly fine veins (*v. s*, text-fig. 50); which all presumably opened into the marginal vein (*v. marg*, text-fig. 50 cf also pl. 34, fig. 1, *mv*).

The dorso-lateral group of superficial veins drained the greater part, or at least the medial (dorsal) part, of the lateral electric field, the external portions of the anterior and lateral parts of the visceral skeleton medially to the lateral electric field, a lateral superficial zone of the occipital region and the upper parts of the shoulder-girdle. It was made up of six distinct veins, the dorsolateral superficial veins, all of which — with the exception of the most anterior one — had a rather decidedly transversal disposition and which all (*v.* ls_1—*v.* ls_6, text-figs. 28, 46—51) poured out into the vena capitis lateralis. In addition to these six dorso-lateral superficial veins there was probably at least a seventh or a few still more posterior ones; but this or these were never independent but united with the sixth one.

We shall now consider the six most anterior dorso-lateral superficial veins more in detail.

The most anterior one of these veins, the dorso-lateral superficial vein 1 (*v.* ls_1, text-figs. 28, 46, 47, 49—51) arose mainly from the superficial part of the visceral skeleton situated postero-medially to the anterior end of the lateral electric field, anteriorly to the orbit and medially (anteriorly) to the n. profundus. Expressed in another way: it drained a postero-latero-superficial portion of the rostral part of the visceral endoskeleton. It went mainly backwards and opened into the preorbital division of the v. capitis lateralis. Rather often it was asymmetrically developed inasmuch as on one side of the median line, generally the right side, it



Text-fig. 51. *Cephalaspis arcticus*? anterior part of cephalic shield showing certain anterior superficial vessels. Magnified.

a. dsm, arteria superficialis postorbitalis; *a. fa*, anterior branch from the a. facialis; *a. fac*, arteria facialis; *a. fp*, posterior branch from the a. facialis; *a. iol*, lateral infraorbital branch of the a facialis; *a. iom*, medial infraorbital branch of the a facialis; *dsf*, dorsal electric field; *lsf*, lateral electric field; *v. cl*, vena capitis lateralis; $v.\ cl_1$, preorbital division of the v. capitis lateralis; *v. la*, vein arisen by the confluence of the dorso-lateral superficial veins 3 and 4; $v.\ ls_1$?, dorso-lateral superficial vein 1; $v.\ ls_2$—$v.\ ls_4$, dorso-lateral superficial veins 2—4; *vv. rs*, rostral veins.

reached much more forwards than on the other. And when this was the case the rostral superficial veins on that side had always become much reduced. In one form (*C. arcticus*?, text-fig. 51; pl. 40, fig. 5) it was on the right side even so strongly developed that it reached almost to the rostral margin.

The dorso-lateral superficial vein following next backwards, i. e. the dorso-lateral superficial vein 2 ($v.\ ls_2$, text-figs. 28, 46, 47, 49—51), arose through the confluence of branches chiefly from the anterior portions of the lateral electric field and from the superficial portion of the visceral skeleton situated between the n. profundus and the n. trigeminus proper. It went postero-dorso-medially and emptied into the preorbital division of the v. capitis lateralis, somewhat behind the dorso-lateral superficial vein 1.

The dorso-lateral superficial vein 3 ($v.\ ls_3$, text-figs. 28, 46—51) drained a portion of the lateral electric field and the superficial portion of the visceral skeleton situated between the n. trigeminus proper and the n. facialis. It was always a rather large vessel, generally considerably larger than the two dorso-lateral superficial veins in front, and it went medially (dorso-medially) and somewhat posteriorly. In the *Cephalaspis*-species it generally entered the posterior part of the orbit, within which it emptied into the v. capitis lateralis. In *Kiaeraspis*, *Benneviaspis* and *Hoelaspis*, on the contrary, it never entered the orbit, but passed upwards and opened into the v. capitis lateralis slightly behind that.

The dorso-lateral superficial vein 4 ($v.\ ls_4$, text-figs. 28, 46—51) was formed mainly by branches from the superficial portion of the visceral skeleton situated between the n. facialis and the n. glossopharyngeus. In addition, however, it received also tributaries from the lateral electric field. Usually it went medially (dorsally) and slightly backwards. The dorso-lateral superficial vein 5 ($v.\ ls_5$, text-figs. 28, 46—50) arose mainly by the confluence of branches from the superficial portion of the visceral skeleton situated between the n. glossopharyngeus and the first branchial branch of the n. vagus, but blood was also carried to it from the lateral electric field. As a rule it went almost straight transversally towards the neurocranium. Finally the dorso-lateral superficial vein 6 ($v.\ ls_6$, text-figs. 28, 46—50) drained a superficial portion of the visceral skeleton which presumably was situated between the first and second branchial branches of the n. vagus, and in addition a posterior part of the lateral electric field. It generally went medially (dorsally) and slightly anteriorly, and in its proximal part there opened into it from behind one or a few more or less small veins, which probably were the dorso-lateral superficial veins of the most posterior parts of the visceral skeleton.

The dorso-lateral superficial vein 6 always emptied its blood into the v. capitis lateralis above the most posterior part of the vestibulum and accordingly rather far behind the dorso-lateral superficial vein 3. The dorso-lateral superficial vein 5 always united with one of the neighbouring dorso-lateral superficial veins, thus with either of the dorso-lateral superficial veins 6 and 4. Only in one form, so far as is yet known, did the dorso-lateral superficial vein 4 reach up to and open into the v. capitis lateralis. In most forms it too united with the neighbouring dorso-latero-superficial veins i. e. with one or other of the dorso-lateral superficial veins 3 and 5. Going more into details, we find that the dorso-lateral superficial veins generally emptied as follows. In one category of forms the dorso-lateral superficial vein 4 united with the dorso-lateral superficial vein 3, while the dorso-lateral superficial vein 5 united with the dorso-lateral superficial vein 6 (text-figs. 49, 50). In another category of forms both the dorso-lateral superficial veins 4 and 5 united the dorso-lateral superficial vein 6, while the dorso-lateral superficial vein 3 carried blood to the vena capitis lateralis only from its own area of drainage (text-figs. 47, 48). Finally, in a third category of forms both the dorso-lateral superficial veins 4 and 5 were instead tributaries to the dorso-lateral superficial vein 3, and this case it was evidently the dorso-lateral superficial artery 6 which emptied blood only from its own area of drainage into the vena capitis lateralis (text-fig. 46).

From the account given and from the figures quoted (text-figs. 28, 46—52) it is easy to see that the dorso-lateral superficial veins 1—6, and perhaps also one or a couple of those following next behind the sixth, like the dorso-lateral superficial arteries and the superficial branches of the a. facialis, alternated in a regular manner with the branchial nerves and thus also with the branchial fossae. We also find that they alternated in a regular way with the electric nerves. Thus they had a metameric disposition. And in this connection it is worthy of notice both that the metameric disposition of the superficial arteries and veins corresponded to the neuromeres and branchiomeres and that the metameric disposition of the vessels, nerves and gills was distinct even in the most anterior part of the prootic division of the head.

Finally among the superficial veins of the dorsal parts of the cephalic shield we have to consider the fourth group, the one which I have called the dorso-medial group. This group consisted exclusively of rather small veins, which all carried blood from the dorsal parts of the half of the neurocranium situated on their side of the median line. The most anterior vein pertaining to this group $v. cl_1$ (text-figs. 46, 47, 49, 50) drained the postero-medial superficial portion of the rostral part of the visceral skeleton and the upper part of the ethmoidal region just behind and laterally to the nasal opening and passed postero-laterally. It constituted the most anterior part of the preorbital division of the v. capitis lateralis; and we shall have the opportunity to return to it below in the description of that vein. The veins of the group that followed next posteriorly ($vv. so, v. dsf_1$, text-figs. 46, 47, 49, 50) arose from the posterior dorsal parts of the ethmoidal region, including the fossa circumnasalis, and further from the dorsal parts of the orbitotemporal region and the anterior part of the dorsal electric field ($v. dsf_1$) situated on this region. They were at least two, but may, in several forms, have attained a number of four or perhaps even more; and all of them went downwards through the dorso-lateral part of the orbitotemporal region to the orbit, within which they opened into the v. capitis lateralis. On account of their place of origin and course they will be called supraorbital veins. Proceeding further backwards, we find the upper parts of the otic region drained by small veins which emptied into the most proximal parts of the dorso-lateral superficial veins 4—6, and by one or a few small veins ($v. ds$, text-figs. 46, 47, 49, 50) which poured out into the v. capitis lateralis. Moreover there was probably in the superficial part of the otic region a rather thick vein ($v. dsf_2$, text-figs. 46, 47, 49, 50) which carried blood from the middle part of the dorsal electric field to the otical vein, which in its turn was a tributary to the occipital vein sinus. Finally, the superficial parts of the occipital region had a great number of fine veins, which all brought blood either to the occipital vein sinus or to the veins which opened into that vein sinus. Among those veins were two (*v. dsf*$_3$, *v. dsf*$_4$, text-figs. 46, 50) which drained the occipital part of the dorsal electric field. More exactly, the most anterior one (*v. dsf*$_3$) of the last-mentioned two veins left the dorsal electric field straight above or slightly antero-dorsally to the canal *nd*$_1$ for the supposed dorsal root of the first spino-occipital nerve and went to the posterior end of the occipital vein sinus, while the other (*v. dsf*$_4$) passed close above the canal *nd*$_2$ for the supposed dorsal root of the second spino-occipital nerve and poured out into a tributary to the lateral occipital vein.

The superficial veins of the lower side of the cephalic shield, if now we turn to these, may be considered to have consisted of two paired groups, one of which comprized the superficial veins from the ventral rim, from the ventral parts of the cornu, from the ventral parts of the shoulder-girdle and from the ventral parts of the postbranchial wall, whereas the other group was composed mainly of the superficial veins which must have been present internally to the scaly covering of the soft tissue that closed the oralo-branchial fenestra. The former of them consisted of fine veins which emptied into the rostral vein sinus and into the marginal vein; the other, on the contrary, was at least in part made up of rather large veins, which, as far as can be judged, went as follows. A longitudinal paired vein, the vena superficialis longitudinalis ventralis (*v. slv*, text-fig. 50), passed from close behind the mouth backwards beneath the entire oralo-branchial chamber, piercing the postbranchial wall through the canal *fy* (text-figs. 33—35). Arrived behind the postbranchial wall it probably united with the marginal vein in the way shown in text-fig. 50. During its passage beneath the oralo-branchial chamber it was probably connected with the marginal vein by means of 10 rather strong transversal superficial veins, the venae superficiales transversales ventrales (v_1—v_{10}, text-fig. 50), which passed beneath each branchial fossa somewhat in front of each branchial opening. The disposition of these veins in the tissue which closed the oralo-branchial fenestra was evidently such that, as far as can be understood, they must have been homologous with the ventral parts of the transversal superficial veins in *Petromyzon* (cf. Cori 1906, pl. XII, fig. 3).

Already several times above we have had the occasion to refer to the rostral vein sinus and the marginal vein. We shall now consider these two vessels in detail.

The rostral vein sinus (*vs. r*, text-fig. 50) was a rather thick unpaired vessel, which was situated within the canal *vs. r* (text-fig. 36; section series F, nos. 39, 42, 49; pl. 51). And thus, as has already been pointed out, it had a transversal position within the most anterior part of the endoskeleton of the cephalic shield and extended on each side of the median line almost as far laterally as the first branchial fossa. In this connection is should also be noticed that it was situated entirely outside the visceral musculature. Blood was carried to it by the rostral group of dorsal superficial veins and by the rostral superficial veins of the ventral rim, and it thus chiefly arose by the confluence of superficial veins. At each lateral end it was presumably continuous with another sinus (*vs. pv*, text-fig. 50) which probably was present around the lateral and posterior borders of the mouth, and which, together with the rostral sinus, seems to have formed an annular sinus around the mouth, an annular sinus that corresponded exactly to the annular labial sinus of the Petromyzontids (cf. TRETJAKOFF 1926, pp. 406—410). The ventral, or more correctly the post-oral, part of that annular sinus was conceivably in direct communication with the v. superficialis longitudinalis ventralis. In view of its relations to the other veins, it cannot be doubted that the annular sinus as a whole belonged to the superficial system of veins. The marginal vein (*v. marg*, *vs. marg*, text-fig. 50) was by its anterior end probably in communication with and merged into a fine anterior branch from the truncus arteriosus, a branch which might have entered the visceral endoskeleton through the canal *va* (text-fig. 36; pl. 51). It went first backwards through the canal *v. marg* in the most ventral part of the visceral endoskeleton (text-figs. 11, 12, 34, 36, 39, 40; section series F, nos. 29—61; pls. 15, 20, 22, 44, 51) medially to the marginal artery and laterally to the branchial fossae, after which it went more postero-medially and entered the cavity *vs. marg* (text-figs. 9—12, 34—36, 39, 40; section series F, nos. 24—55; pls. 15, 22; pl. 23, fig. 3; pls. 51—53, 58) between the visceral endoskeleton and the endoskeletal shoulder-girdle. Behind the cavity *vs. marg* it must have retained its postero-medial direction and have passed close behind the ventral part of the postbranchial wall. Finally, rather far medially behind the postbranchial wall it probably united with the vena superficial longitudinalis ventralis and emptied together with this into the ventral jugular vein in the way shown in text-fig. 50.

The marginal vein during its way backwards soon became a rather wide vessel and continued to widen backwards until opposite the interbranchial septum 4, where, at the entrance into the cavity *vs. marg*, it probably became wide again and even wider than more anteriorly; but it soon diminished in width again when it left this cavity and it is probable that from there it gradually became narrower backwards. In this connection it is also worthy of notice that within the canal *v. marg* it had distinct dilatations corresponding to each one of the interbranchial septa 1, 2 and 3. It received its blood from the superficial parts and the interior of the cornu, from the superficial parts and the interior of the shoulder-girdle, and finally from the superficial parts and the interior of the ventral portion of the visceral skeleton. As we have found, it was probably connected with the vena superficialis longitudinalis ventralis by means of the venae superficialis transversales ventrales which traversed the canals v_1—v_{10} (text-figs. 4, 33, 34, 36, 39—41, 50; pls. 20, 22, 51, etc.).

On account of its position and on account of its relations to the superficial system of veins it seems highly probable that the marginal vein, like the rostral vein sinus, belonged to the superficial system of veins, though, owing to the specialisation of the cephalic shield, it had come to occupy such a position that it became very wide and sunk somewhat deeper into the endoskeleton than most other superficial veins, except the rostral vein sinus. In fact it seems highly probable that it was homologous with the vena superficialis longitudinalis dorsalis of *Petromyzon* (cf. Cori, 1906, pl. XI).

From what has been set forth here we have found that the Cephalaspids possessed a very complicated system of superficial veins, a system which in several important points was highly suggestive of that of the Petromyzontids.

After having considered the superficial system of veins, we now turn to the other veins of the cephelic shield which were the v. capitis lateralis with its tributaries from the endocranium, and further the v. cardinalis anterior (v. capitis medialis) and the v. jugularis ventralis.

The v. capitis lateralis, as we have seen, arose as a superficial vein from the ethmoidal region and the rostral part of the visceral skeleton somewhat antero-laterally to the nasal opening (*v. cl*$_1$ text-figs. 28, 46, 47, 49—51), and went first usually postero-laterally and received the dorso-lateral superficial veins 1 and 2. Behind these veins it took a posterior or a posterior and somewhat medial direction and began to penetrate deeper into the endoskeleton. After continuing in this direction for a more or less long distance, it entered the orbit at the anterior end, but close anteriorly to the orbit it had in certain cases a rather distinct swelling. Within the orbit (*v. cl*, text-fig. 46—51) it certainly passed backwards and slightly laterally rather close to the interorbital wall; and during this part of its course it received the supraorbital veins (*v. so*, *v. dsf*$_1$) and probably also a vein from the cavum cerebrale cranii, a vein which traversed the canal *v. pt* (text-figs. 16, 17, 21, 22, 24; section series A, nos. 88—90, 93—94; section series C, nos. 1—9, 26; section series D, nos. 4—9), and which perhaps may have corresponded to the pituatary vein of fishes although it did not leave the cavum cerebrale at the fossa hypophyseos, but somewhat behind that (cf. Allis 1909 a, pp. 183—208; 1911 a, p. 291; 1914; 1918 a; 1919; 1922 a; 1922 b; Allen 1905, p. 81; Gegenbaur 1872, pp. 75—79; Lehn 1918, p. 380; O'Donoghue 1914, pp. 440—441; Stensiö 1921, pp. 62, 177—180; 1922, p. 179; 1923, pp. 1244, 1262—1268; 1925 a, pp. 52—71; etc.). In the *Cephalaspis*-species it had in the hindmost part of the orbit, just before it entered the otic region, yet another tributary which, as we have seen, was the dorso-lateral superficial vein 3 or a trunk formed by the union either of the dorso-lateral superficial veins 3, 4 and 5 or of the dorso-lateral superficial veins 3 and 4.

After leaving the orbit at the posterior end, and usually rather high above the floor, the v. capitis lateralis passed backwards within the endoskeleton of the otic region, dorsally to the vestibular division and laterally to the anterior and posterior semicircular divisions of the labyrinth cavity, and during this part of its course it had a slight medial bend. In the posterior part of the otic region it curved downwards and emerged from the neurocranium. More exactly, it had its exit from the neurocranium at the posterior end of the otic region somewhat latero-dorsally to the place at which the n. glossopharyngeus entered the labyrinth cavity. After it thus had definitely left the neurocranium it must have passed downwards and somewhat medially behind the postbranchial wall in order to join there the anterior cardinal vein (v. capitis medialis) of its side, probably approximately in the way shown in my restoration of the venous system published in text-fig. 50.

During its passage through the otic region the v. capitis lateralis perhaps received a number of small tributaries from the vestibular division of the labyrinth cavity, tributaries which traversed the canals $v. lab_1$—$v. lab_5$ (section series A, nos. 57—67; section series B, nos. 18, 24, 25, 27—29; section series C, nos. 65—70; section series D, nos. 12—14, 19, 20, 26). But it is also not impossible that these canals instead transmitted nutritive arteries to the v. capitis lateralis and to the dorso-lateral parts of the otic capsul and in addition dorsal nerve branches from the n. facialis and the n. glossopharyngeus. Besides these possible tributaries the v. capitis lateralis had in the otic region also a number of other more important ones all of which, however, except the occipital vein sinus, have been dealt with in detail above. For all these, except the occipital vein sinus, it may therefore be sufficient here to refer the reader to text-figs. 46—51.

The occipital vein sinus (*vs. oc.* text-figs. 23—28, 46, 48, 50; section series A, nos. 27—46; section series B, nos. 2—16; sectton series C, nos. 49—73; section series D, nos. 1—40; pls. 25, 26, 49; pl. 54, fig. 1; pl. 55) was a wide vessel situated in the endocranium at the transition between the occipital and otic regions. Postero-dorso-medially it was produced backwards into a long corner, and into this corner opened the myelonal vein 1 ($v. spi_1$, text-fig. 50) and probably also a thick vein from the posterior parts of the dorsal electric field ($v. dsf_3$, text-fig. 50). Just laterally to this posteriorly produced corner there poured out into it a thick vein, the lateral occipital vein (*v. ol*, text-figs. 23—26, 46, 50), which went forwards through the most lateral part of the occipital region of the endocranium and which arose through the confluence of the most posterior superficial veins belonging to the dorso-medial group with the myelonal vein 2 ($v. spi_2$, text-figs. 46,

50) and the most posterior vein (*v. dsf*$_4$, text-figs. 46, 50) from the dorsal electric field. The lateral occipital vein was — at least in certain forms, such as *C. hoeli* (*v. ol*, text-figs. 23, 25, 26) — in communication with its fellow of the opposite side by a transversal commissure (*v. dc*), which was situated in the hindmost part of the occipital region of the endocranium above the most posterior part of the cranial cavity and thus in fact rather superficially.

Anteriorly to its postero-medial corner the occipital vein sinus received on its medial side near its bottom the rather thick v. cerebralis posterior (*v. cp*, text-figs. 46, 50), which arose in the posterior parts of the cavum cerebrale cranii and, as usual, traversed the most dorsal division of the vagus canal. From the otic region a thick vein, the otical vein (text-figs. 46, 50), seems to have passed backwards through the dorsal part of the otic region between the canalis semicircularis posterior and the cavum cerebrale to the anterior dorso-medial part of the occipital vein sinus. The otical vein probably arose through the confluence of two branches, one of which seems to have been of a superficial sort and to have come from the middle part of the dorsal electric field (*v. dsf*$_2$), while the other (*v. vest*, text-figs. 46, 50) may have drained the labyrinth cavity or at least certain dorso-medial or medial parts of that cavity. Finally, it is quite clear that a great number of superficial veins belonging to the posterior ones of the dorso-medial group carried blood to the occipital vein sinus.

Laterally, the occipital vein sinus opened with a rather narrow duct into the v. capitis lateralis from the medial side, close anteriorly to or just at the place at which the v. capitis lateralis left the otic region (text-figs. 26, 46, 48, 50).

On the ventral or ventro-posterior side of the occipital vein sinus there issued certain rather fine veins in a more or less straight ventral direction, veins which probably went down to and joined the v. cardinalis anterior of their side. This fact, together with its relations otherwise, shows that the occipital vein sinus probably was a structure arisen from collateral branches of parietal veins.

From the facts given here concerning it and its tributaries it is clear that the v. capitis lateralis of the Cephalaspids must have been homologous with the similarly named vein in Cyclostomes and in fish larvae. And further it is easy to see that, both with regard to its extension and position and with regard to the fact that it persisted fully unchanged in the adult, the v. capitis lateralis of the Cephalaspids was highly suggestive of that in *Petromyzon* (cf. CORI, 1906; HATTA 1922; DE BEER 1924; 1926). In this connection it is worthy of notice that in *Petromyzon* there is an occipital vein sinus (cf. DE BEER 1924, p. 326, fig. 38; CORI 1906, pp. 50—51, pl. XI, pl. XII, fig. 2) which probably is homologous with that of the Cephalaspids and that thus also with regard to this special tributary the v. capitis lateralis of the Cephalaspids was in a striking way in accord with that of *Petromyzon.*

On account of its relations to the superficial veins in the Cephalaspids it seems not improbable that the v. capitis lateralis originally pertained to the superficial system of veins; and since it was present and played such an important part even among such old primitive vertebrates as the Cephalaspids, it seems conceivable to me that it was a very old structure, probably even as old as the v. cardinalis anterior (v. capitis medialis; cf. De Beer 1924, p. 339).

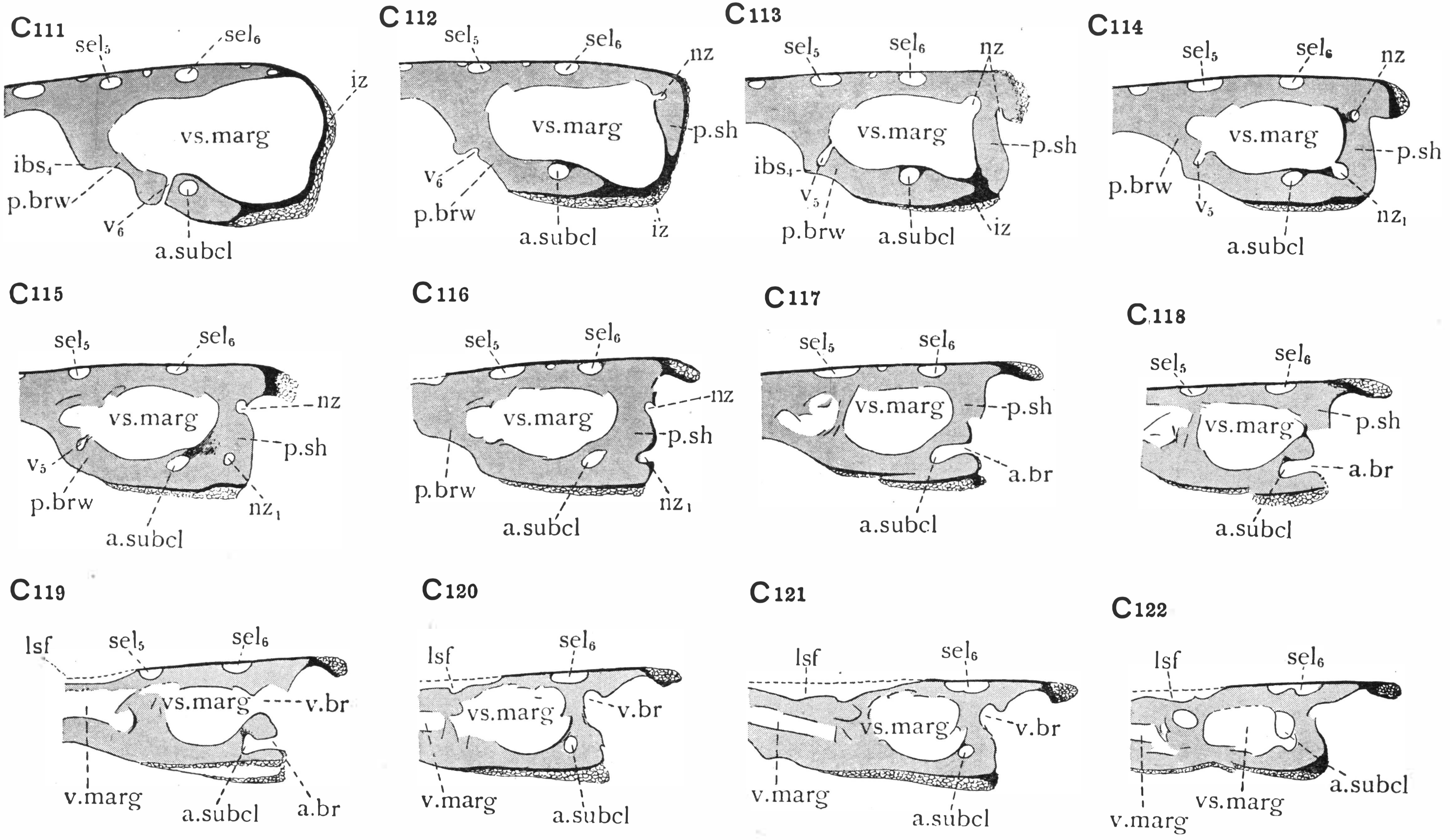
A paired v. cardinalis anterior (v. capitis medialis) was certainly present. If this vein arose as far forwards as beneath the endocranium, it would have passed backwards along the ventral surface of the cranial base. And in that case it might have left the oralo-branchial chamber either together with the aorta or with the oesophagus. It is more probable, however, that it did not reach further forwards than to the posterior surface of the postbranchial wall, and that it thus was strikingly short. Close behind the postbranchial wall, and accordingly about at its presumed anterior end, it received the v. capitis lateralis of its side (text-fig. 50). Into it emptied further a number of anterior parietal veins, and among these were also those from the collateral branches of which the occipital vein sinus, as has been pointed out, probably arose.

The most median subbranchial parts of the head must have been drained by a system of veins which perhaps joined into a median unpaired v. jugularis ventralis, as in the Petromyzontids. How I imagine this vein to have been, is elucidated by text-fig. 50 (v. jug. v).

The facts brought forward here show quite clearly that the vascular system of the Cephalaspids, though specialized in certain respects, nervertheless was of a type which among recent forms is found only in the Cyclostomes and among these particularly in *Petromyzon.*

Endoskeletal shoulder-girdle.

The endoskeletal shoulder girdle is a continuous skeletal piece, which, as has already been pointed out (pp. 20—29 above) forms part of the endoskeletal component of the cephalic shield, constituting the posterolateral part of that (text-figs. 5, 7—12). More exactly, it has the following relations to the other parts of the endoskeletal component of the cephalic shield. It is continuos with the antero-lateral part of the occipital region dorso-medially, with the visceral endoskeleton anteriorly and medially, and with the endoskeleton of the cornu of its side laterally (text-figs. 5, 7, 8, 9—12, 33—35, 52; pls. 9, 10; (section series F, nos. 24—63). Within the transitional part between it and the visceral endoskeleton there is always the big cavity *vs. marg*, which, as we have found, was occupied by a widened part of the marginal vein. Postero-medially it



Text-fig. 52. *Cephalaspis hoeli.* Series of rostro-caudal sections through the endoskeletal shoulder girdle (posterior parts of the sections 111—122 of the section series C). Cartilage with a light shading, bone with continous lines. C 111 the most medial, C 122 the most lateral of the sections. Magnification about $^{7,5}/_{1}$.

a. br, canal for the brachial artery; *a. subcl*, canal for the a. subclavia; *ibs*$_4$, interbranchial septum 4; *iz*, interzonal part of the cephalic shield (consisting only of exoskeletal bone); *lsf*, lateral electric field; *nz*, canal for a nerve to the pectoral fin; *nz*$_1$, canal either for a nerve or a vein, or for both; *p. brw*, postbranchial wall; *p. sh*, endoskeletal shoulder-girdle; *sel*$_5$, *sel*$_6$, canals for the electric nerves 5 and 6 to the lateral electric field; *v*$_5$, *v*$_6$, canals for the ventral transversal superficial veins 5 and 6; *v. br*, canal probably for a brachial vein; *v. marg*, canal for the marginal vein; *vs. marg*, cavity for a posterior part of the marginal vein.

passes over into the lateral wall of the interzonal part of the cephalic shield, a part which is built up exclusively of exoskeleton (text-figs. 9—12, 33—35, 52; section series A, nos. 159—167; section series F, nos. 24—63), and owing to this the pectoral sinus is surrounded by skeleton not only anteriorly and laterally but also medially (cf. text-figs. 33—35). Text-figs. 52 and sections nos. 24—63 of section series F elucidate more in detail what has been set forth here concerning the position and relations of the endoskeletal shoulder-girdle.

Except in *Boreaspis rostrata*, in which probably it was ossified throughout, the endoskeletal shoulder-girdle consisted in all the forms known of the same sort of cartilage as the other parts of the endoskeletal component of the cephalic shield. It was always lined with a thin layer of perichondral bone (respectively periostal bone when it was ossified throughout) on the posterior surface exposed in the pectoral sinus, on the surface which formed part of the boundary of the cavity *vs. marg* and in all the canals which traversed it.

The most dorso-medial part of the endoskeletal shoulder-girdle is pierced by a rather fine canal, *nz* (text-figs. 33—35, 52), which has such a position that it must have transmitted a structure that came from above and medially in the most anterior part of the trunk and passed to the antero-dorso-medial part of the pectoral fin. And from this it is easy to understand that the canal gave passage to a nerve which went to the antero-dorso-medial part of the pectoral fin.

Somewhat medially to the canal just described there is another and generally wider canal (nz_1 text-figs. 12, 33—35, 52; section series F, nos. 34—44), which, like the former, perforated the postero-medial part of the endoskeletal shoulder-girdle in a direction transversal to the longitudinal axis of the fish. This canal, nz_1, has its internal (medial opening) close posteriorly to and below the level of the subclavian ridge, while its external opening is situated close behind (medially) to the opening of the canal for the arteria brachialis (*a. br*). What its function may have been, it is not possible to decide with full certainty, but it is very probable that it transmitted a vein from the lower side of the pectoral fin to the marginal vein. In addition it may perhaps also have been traversed by a nerve to the lower side of the pectoral fin.

Within the most dorso-lateral part of the endoskeletal shoulder-girdle there is always found a rather wide canal (sel_6, text-figs. 9—12, 13, 34, 52), which comes from the occipital region and passes postero-laterally to the posterior part of the lateral electric field, which, as we have seen, generally extends backwards on the cornu. This canal was the canal for the sixth electric nerve to the lateral electric field.

The canal for the arteria subclavia (*a. subcl*, text-figs. 9—12, 36, 39, 40, 44, 52; section series A, nos. 163—167; section series F, nos. 11—48; pls. 20, 22, 28; pl. 46, fig. 1; pl. 47, fig. 1; pls. 51—53, 58), when it left the postbranchial wall, entered, as we have found, the basal part of the endoskeletal shoulder-girdle proper, which it traversed in a lateral direction, after which it arrived in the antero-medial part of the cornu of its side. Rather soon after its entrance into the endoskeletal shoulder-girdle it gave off a wide branch (*a. br*, text-figs. 12, 35, 36, 39, 40, 44, 52; section series A, nos. 163—166; section series F, nos. 34—45) backwards to the antero-medial part of the pectoral sinus, a branch which, as has been pointed out, must have lodged the artery that supplied the pectoral fin, that is the arteria brachialis. Within the cornu the a. subclavia divided into two branches, one of which (*a. c*, text-figs. 12, 36, 39, 40, 44, 52) went to the cornu of its side, while the other (*a. marg*, text-figs. 12, 36, 39, 40, 44, 52; pls. 20, 22, 44, 51) turned forwards and traversed the most ventro-lateral part of the visceral endoskeleton laterally to the canal, *v. marg*, for the marginal vein. As has been shown above, (pp. 183—186, 226—228) the former of these two branches lodged the a. cornualis, the latter the a. marginalis.

Finally, there is still one canal through the endoskeletal shoulder-girdle which remains to be considered here. This canal (*v. br*, text-figs. 5, 9—11, 34, 35, 39, 40, 52; section series F, nos. 28—33; pl. 10 *v.* br_2, pl. 54, fig. 2) leads from the cavity *vs. marg* to the dorso-median part of the pectoral sinus. As far as can be judged, it transmitted a vein which drained at least the dorsal side of the pectoral fin.

The posterior surface of the endoskeletal shoulder-girdle exposed in the pectoral sinus (text-fig. 35) is concave in the transversal direction; and since, apart from this general concavity, it seems to have been rather smooth without any pronounced raised parts or fossae in or against which the pectoral fin could have articulated, it is not possible to decide where the articulation between it and the pectoral fin took place, nor possible to draw any conclusions concerning the endoskeleton of the pectoral fin.

Owing to its position far postero-laterally and to the facts that it is continuous with the shoulder-girdle and is supplied by a branch of the a. subclavia, it seems highly probable that the cornu does not belong to the head, i. e. is a portion of the visceral skeleton, but that it simply is a posteriorly, postero-laterally or laterally produced part of the shoulder-girdle. Throughout this paper, therefore, it has been considered as such. Accordingly the endoskeleton of the shoulder-girdle of the Cephalaspids would comprise not only what has been described here as the endoskeletal shoulder-girdle proper but in addition also the endoskeleton of the cornu.

Although the endoskeletal shoulder-girdle of the Cephalaspids, taken in this wide sense, differs in several respects from that in fishes and Tetrapods nevertheless, from the facts known at present concerning it, it is fully evident that both with regard to its position behind the branchial region and to its relations to the vessels and nerves it has so many important features in common with that of fishes and Tetrapods that we are forced to the conclusion that it is homologous with this. As far as can be judged, the Cephalaspids would thus have a true shoulder-girdle and a true pectoral fin. And as we shall see from the comparative account below, this was probably the case with several other groups of Ostracoderms too.

Certain remarks on the exoskeleton.

The minute structure of the exoskeleton has been dealt with above in the general account of the cephalic shield (pp. 32—41). Here, however, it should be particularly emphasized that the most basal part of the basal layer of the exoskeleton probably is of perichondral (or else periostal) origin and therefore, strictly speaking, presumably does not pertain to the exoskeleton (cf. p. 40—41).

In consequence of its extent, the exoskeleton of the cephalic shield comprises parts which pertain to the neurocranium, to the visceral skeleton, to the shoulder-girdle and to the most anterior part of the trunk.

The scales which covered the soft tissues that closed the oralobranchial fenestra belonged to the visceral skeleton.

Lateral sensory canal system and electric fields.

The lateral line system is known only on the cephalic shield on which it consists of narrow, shallow grooves of a similar type as those in *Tremataspis*, though not so frequently interrupted as those. Despite the fact that fragmentary remains of it may be seen in many forms, among others in *Hemicyclaspis* (*Cephalaspis*) *murchisoni* and *Cephalaspis salweyi*, it is nevertheless rarely found in a somewhat complete state of preservation. Up till now in fact it is known in any detail only in one specimen of each of the species *Benneviaspis holtedahli* and *Hoelaspis angulata* from the Spitsbergen Downtonian. It had always a very superficial position, so that it could give rise to distinct grooves only in those forms which have the superficial layer well developed. In those forms which have that layer in a reduced state, on the contrary, it was probably situated entirely in the soft tissue outside the exoskeleton.

It should be noticed that I shall use in this description the same terminology as in my previous works (cf. STENSIÖ 1921, p. 103; 1922, p. 192; 1923, pp. 1257—1259; 1925 a, p. 114, 1925 b, p. 146; 1926).

In *Benneviaspis holtedahli* it is evident (text-fig. 76) that the lateral line system of the cephalic shield, at least in certain specimens, was somewhat differently developed on the right and left sides. So far, however, it has proved impossible to decide whether this was a condition peculiar only to that species or whether it occurred also in other forms.

According to our present knowledge of it, the lateral line system of the cephalic shield consists of the following grooves: a paired infraorbital groove, a paired cephalic division of the main lateral line, two paired rather long transversal grooves, and finally two short paired transversal grooves laterally to the anterior half of the dorsal electric field.

The infraorbital groove (*ifc*, text-figs. 76, 77), when typically developed, stretches from the ventro-laterally margin of the orbital opening antero-ventro-laterally to the medial margin of the anterior part of the lateral electric field, and it seems not impossible that it continued even further antero-latero-ventrally so that it ended on the exoskeletal plates that covered the anterior part of the lateral electric field. As far as can be judged, therefore, it seems to be situated almost straight above the canal (V_2) for the trigeminus proper, and so everything indicates that it was supplied by the lateralis fibres which accompanied the n. trigeminus proper, that is to say by the lateralis fibres which, if I am right, were homologous to the n. buccalis lateralis of fishes. Before leaving it, attention should be called to the fact that in the specimen of *Benneviaspis holtedahli* figured in text-fig. 76 A the infraorbital groove was represented on the left side only by a short proximal part close to the orbital opening, a part which was continuous with the transversal groove lettered *cm*, while on the right side, on the contrary, it was developed in the typical way.

The cephalic division of the main lateral line (*lc*, text-figs, 76, 77) is always present and, as usual, it has a chiefly longitudinal course on the cephalic shield. In the specimen of *Benneviaspis holtedahli* in which it could be studied (text-fig. 76) it consists on the right side of three somewhat irregularly situated pieces, while on the left side it is represented merely by two pieces. In the specimen of *Hoelaspis angulata* in which it was preserved (text-fig. 77) it consists, at least on the right side, of only one rather long piece. Mostly it seems not to reach backwards to the posterior margin of the cephalic shield, but in the specimen of *Benneviaspis holtedahli* here in question it is, however, clear that on the right side it went as far back as the posterior part of the postero-lateral angle and that from this it continued on to the scale-covered part of the trunk. On account of its position and extension it is fully evident that it can have been innervated only by lateralis fibres which accompanied the n. glossopharyngeus and the n. vagus, i. e. only by postotic lateralis fibres.

For the study of the two long transversal grooves we first consider the specimen of *Benneviaspis holtedahli* figured in text-fig. 76 A. In that specimen both of them ($cmm_1 + cmm_2$ and cm) are clearly seen. The anterior one (cm) of them is somewhat differently developed on the right and left sides. On the right side it reaches from a point somewhat postero-latero-ventrally to the orbit for a certain distance in an antero-latero-ventral direction, though by far not down to the lateral electric field. On the left side, on the contrary, it seems to be continuous with the short infraorbital groove — the only part present of the left infraorbital groove — and it thus reaches from a point slightly latero-ventrally to the orbital opening latero-ventrally and slightly posteriorly, but like the right groove it ends already rather far dorso-medially to the lateral electric field. As far as can be judged from its course and position, this groove (*cm*) was innervated by lateralis fibres which accompanied the n. facialis; and it is therefore likely that it corresponds to one of the lateral sensory canals of the cheek of fishes, that is, either to the jugal canal or to the preopercular canal (cf. STENSIÖ 1921, pp. 76—77, 103; 1923, p. 1258; 1925 b, pp. 178—179).

The other long transversal groove in the specimen in question of *Benneviaspis holtedahli* (text-fig. 76 A) is situated on the posterior part of the cephalic shield and consists of two parts, a dorsal one (cmm_1) and a ventral one (cmm_2). The former of these parts extends from the posterior portion of the dorsal electric field almost straight laterally to the cephalic division of the main lateral line, with which it is united. The latter part, on the contrary, reaches from the vicinity of the cephalic division of the main lateral line latero-ventrally almost to the medial margin of the posterior part of the lateral electric field and is as a whole situated somewhat in front of the dorsal part. From its position and relations it cannot be doubted that the long transversal groove just described was innervated by postotic lateralis fibres, a condition which indicates that it must be homologous either with the supratemporal commissure or with the posterior head-line of pit-organs of fishes (cf. ALLIS 1889, pp. 502—509, pl. 42; STENSIÖ 1925 a, p. 144; 1925 b, pp. 148—149; etc.). And consequently in *Tremataspis* it has its equivalent in the groove that I have denoted in text-fig. 83 by the letters *cmm*. Finally in *Palaeaspis* it would correspond either to the second or to the third of the transversal commissural canals following behind the suprapineal one (cf. STENSIÖ 1926).

If, after the description of the condition of the long transversal grooves in *Benneviaspis holtedahli*, we turn to the specimen of *Hoelaspis angulata* figured in text-fig. 77 we find at once that this differs rather much from the specimen of *B. holtedahli* dealt with by the total absence of the anterior long transversal groove *cm*. The posterior long transversal groove ($cmm_1 + cmm_2$), on the contrary, is for the mot part like that in *Benneviaspis holtedahli*, except that the lateral part of it is continuous with the cephalic division of the main lateral line at its dorsal end.

Finally the two short transversal grooves are to be observed both in *Benneviaspis holtedahli* and *Hoelaspis angulata* (*pc*, *cmm*, text-figs. 76, 77); and it is characteristic for both of them that they are situated close to the anterior half of the dorsal electric field. More exactly, the anterior groove (*pc*) regularly lies close postero-dorsally or postero-dorso-medially to the orbital opening at the anterior end of the dorsal electric field and close behind the pineal opening, while the posterior one (*cmm*) follows somewhat more backwards. Their direction may be either rather straight or more or less obliquely transversal. From its position it is easy to conclude that the anterior one (*pc*) of them certainly must have been innervated by prootic lateralis fibres, perhaps by branches from the n. ophthalmicus lateralis and therefore that it represents either a posterior part of the supraorbital canal or the anterior head-line of pit-organs of fishes or, what is more probable, the suprapineal canal of the Pteraspids and the suprapineal sensory canal organs in *Petromyzon* (cf. STENSIÖ 1926). Attention should also be called here to the fact that an exactly corresponding short groove occurs in *Tremataspis* (*pc*, text-fig. 83). Concerning the posterior short transversal groove (*cmm*) it is dificult to conclude whether it was supplied by lateralis fibres which had their exit from the cranial cavity together with the n. facialis or by lateralis fibres which emerged together with the n. glossopharyngeus. Most brobably is, however, that the latter alternative was the true one; and if it was so, the groove would of course be homologous with the middle head-line of pit-organs of fishes and the first cross-commissural canal behind the suprapineal one in *Palaeaspis* (STENSIÖ 1926). In *Tremataspis* it has an exact equivalent in a short groove just laterally to the anterior half of the dorsal electric field (*cma*, text-fig. 83).

In none of the typical cephalaspids studied have I been able to observe any distinct undoubted traces of a supraorbital canal, but despite this it is not quite inconceivable that certain parts of such a canal were present but in such a reduced state that they lay very superficially and did not cause any markings on the cephalic shield. In *Didymaspis*, on the contrary, I have found a paired sensory canal situated transversally in front of the nasal opening (Brit. Mus. specimen P. 12659), a canal which corresponds exactly to the most rostral portion of the infraorbital canal of *Tremataspis* and which, like that portion, perhaps may have been supplied by a nerve corresponding to the n. ophtalmicus lateralis of fishes (cf. text-fig. 83). In this respect, therefore, *Didymaspis* appears to be more in accord with *Tremataspis* than with the typical Cephalaspids.

As is obvious from the account just given of it the lateral line system of the Cephalaspids in most chief points agrees very well with that of *Tremataspis*. By the presence of a homologue of the suprapineal groove and by the presence of the long transversal grooves, however, it is also to a certain degree in accord with that in the *Pteraspidae* and *Petromyzon* (cf. STENSIÖ 1926); and because of that there is reason to believe that it has been derived from a Pteraspid-like one. Accordingly it is conceivable that it is in a highly specialized and partly reduced state (cf. also the description of the *Trematas pidae* below in the present work).

The electric fields, which have been frequently referred to above, are depressed areas on the dorsal side of the cephalic shield (text-figs. 2, 3, 5, 28, 46, 49, 52, 53, 56—58, 61, 62, 64, 65, 67, 68, 71, 76—79; most of the plates). They reach downwards into the external parts of the endoskeleton and are bounded basally by a layer of bone which is continuous with the most basal part of the basal layer of the exoskeleton and which belongs to the endoskeleton. In several of the forms from Britain and Norway they are found to be covered by small bone plates (cf. p. 23), but in the Spitsbergen forms no such plates have been found, probably owing to the fact that these plates had loosened and fallen away already before the specimens became embedded in the rock[1].

As we have seen, there are in all Cephalaspids one unpaired and one paired electric field the former of which was called the dorsal electric field, the latter the lateral electric field.

The dorsal electric field (*dsf*, text-figs. 2, 3, 49, 51, 53, 54, 57, 61, 64, 65, 67, 71, 74, 76—79; section series A, nos. 11—99; section series B, nos. 1—41; section series C, nos. 1—29; pls. 1, 3, 13, 17 and several of the others) is always situated above the median parts of the neurocranium behind the pineal opening. More exactly, it has its anterior end close behind the pineal opening and its posterior end more or less far back on the occipital region. It is always longer than it is broad, and its maximum width is generally less than the distance between the commissural divisions of the labyrinth cavities. The anterior end is mostly truncated, whereas the posterior end is more or less pointed or rounded. Otherwise it may in different species exhibit rather considerable variations in its configuration.

The lateral electric field (*lsf*, text-figs. 2, 3, 5, 28, 46, 49, 53, 56—58, 61, 64, 65, 67, 68, 71, 74—79; section series C, nos. 100—130; pls. 21, 29, 31, 49 50 and several of the other plates) lies close to the lateral margin of the cephalic shield and stretches from the lateral portion of the rostral part of the visceral endoskeleton backwards to the shoulder-girdle. In those *Cephalaspis*-species, and in other forms which have long broad cornua, it always reaches more or less far backwards on the cornu of its side; in those *Cephalaspis*-species and other forms, on the contrary, in which the cornua are long but narrow and more or less circular in transversal section, it generally ends on the very anterior part of or just anteriorly to the cornu of its side. Finally in those

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[1] According to what is distinctly shown by certain specimen in the British Museum these plates consist of basal, middle and external layers, exactly as the other parts of the exoskeleton of the cephalic shield.

forms which have much reduced cornua, such as *Kiaeraspis* (text-figs. 3, 5, 79), it has its posterior part produced medially and situated rather far medially (dorso-medially) to the anterior part of the corresponding cornu and accordingly considerably more medially than in the other two categories of forms. Since *Benneviaspis* (text-fig. 76 A), *Hoelaspis* (text-fig. 77) and *Boreaspis rostrata* (text-fig. 78) exhibit conditions wich in this respect seem to be intermedially between the conditions in *Kiaeraspis* and those in the two other categories of forms, it is probable that those in *Kiaeraspis* have arisen from those in the other categories of forms, i. e. primarily from *Cephalaspis*-like ones.

Except in *Eukeraspis* in which it is said to consist of six isolated divisions (Lankester 1870, text-fig. 31, p. 58; Woodward 1891 a, text-fig. 27, p. 193)[1], the lateral electric field is in all forms known hitherto a continuous depression. It is always several times as long as it is broad, and at least in several cases its maximum width falls in its anterior part. The anterior end is more or less obtusely pointed or rounded; the posterior end may be rounded too, but is often rather pointed. While the lateral (latero-ventral) margin as a rule, at least in most forms, runs concentrically or chiefly concentrically with the lateral margin of the cephalic shield and is without any very conspicuous irregularities, the medial (dorso-medial) one may not rarely, particularly in the anterior and posterior parts, have sharp bends or corners in the way shown in text-figs. 53, 57, 58, 61, 68, 71, 76—78.

After this general description of the position and configuration of the electric fields, we pass to an examination of their interior.

The dorsal electric field, as displayed by several of the section series (section series A, nos. 11—99; sertion series B, nos. 1—41; section series C, nos. 1—29) is rather deep. Its deepest part is situated in the otic region just behind the division of the cavum cerebrale cranii that lodged the cerrebellum and above the anterior part of the division of the same cavum that lodged the medulla. To this part of it there leads from the ventro-medial part of the commissural division of the labyrinth cavity of each side a thick canal lettered *des* in the figures (text-figs. 18, 19, 23, 26, 27; section series A, nos. 50—60; section series B, nos. 17—23; section series C, nos. 1, 23—40; section series D, nos. 30—35), a canal which, as we have seen, transmitted a nerve and probably also a vein. After arriving into the deepest part of the dorsal electric field, this canal *des* unites with its fellow from the other side (text-fig. 27); and from the common trunk or space thus formed there issue wide canals on the bottom of the dorsal electric field both forwards and backwards (pl. 39).

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[1] As far as I have been able to find on specimens in the British Museum, however, the lateral electric field of *Eukeraspis* seems to be subdivided only into four divisions.

These wide canals divide into a number of rather fine more superficial ones (section series B, nos. 1—41; pl. 17), which in their turn break up into very numerous still finer branches which lie superficially to all the others (section series B, nos. 1—41; pl. 3, fig. 3).

The lateral electric field is less deep than the dorsal one. As we have found, it is entered from the medial (dorso-medial) side by six thick nerve canals (sel_1—sel_6, text-figs. 28, 46, 47; many of the plates), which all issue from the vestibular division of the labyrinth cavity and traverse the visceral endoskeleton in antero-lateral, lateral and postero-lateral directions. The two most anterior of these nerve canals (sel_1, sel_2) are united with each other at least as far forwards as until just antero-laterally to the orbit as in the *Cephalaspis*-species (pls. 17, 21, 27—29), or further forwards, even as far as close or just to their entrance into the lateral electric field (*Benneviaspis*, *Hoelaspis*, *Boreaspis rostrata*, *Kiaeraspis*; cf. text-fig. 28 and pls. 14, 42, 45, 49, 50). How the six nerve canals in question went in relation to the other nerve canals and to the canals for the vessels is well shown by the figures cited and has also been dealt with above on pp. 171—174 and on p. 182. Here it need only to be mentioned that they have a metameric disposition and that they probably belong to the mandibular, the hyoid and the four first postotic metameres respectively. That the electric nerves within the field broke up into a great number of branches which anastomosed with each other is well understood from pls. 17, 21, 27—30, pl. 31, fig. 3 and pls. 45, 49 and 50 which show the mode of branching of the most terminal parts of the electric nerve canals.

As is evident from the nerve canals leading to them, the electric fields were innervated by thick and strong nerves which broke up into an excedingly great number of terminal branches. These nerves which have been referred to above as the electric nerves, must, as is easily understood, have been composed of a special sort of fibres which according to their presumed function may be called electric fibres. Above we have already had the opportunity of considering the system of these nerve fibres (cf. pp. 90—92 above); but it may nervetheless be appropriate to recapitulate here the most important of what was said about it.

It is not very likely that there were any postotic electric nerve fibres, but, if there were, these fibres must have been associated with the glossopharyngeus and vagus roots and those of them for the dorsal electric field would have reached this through the canal *dx* (text-figs. 15—23) and the upper part of the canal *des* (text-figs. 18, 19, 23, 26, 27; section series A, nos. 49—52; section series D, nos. 17—23), while those for the lateral electric field would have accompanied the n. glossopharyngeus to the vestibular division of the labyrinth cavity.

Except these possible postotic ones all the electric nerve fibres were prootic and left the cavum cerebrale cranii closely associated with the ramus anterior of the n. acusticus, the roots of the n. facialis and the prootic lateralis roots and arrived together with these in the vestibular division of the labyrinth cavity (text-figs. 32, 43). Well within that division of the labyrinth cavity they soon divided into two groups (text-fig. 43) — a dorsal one which passed upwards and medially in the groove *dsv* and through the canal *des* (text-figs. 18, 19, 23, 26, 27; section series A, nos. 50—60; section series B, nos. 17—23; section series C, nos. 1, 23—40; section series D, nos. 30—50) to the dorsal electric field, and a lateral one which followed the floor of the vestibular division of the labyrinth cavity laterally and which soon broke up into six thick nerve-trunks which entered and traversed the canals sel_1—sel_6 to the lateral electric field. The two anterior ones of these nerves to the lateral electric field remained, however, closely associated with each other during a considerable stretch forwards, in any case at least as far forwards as the antero-lateral corner of the orbit. If there were any postotic electric fibres, and if any of these had entered the vestibular division of the labyrinth cavity together with the n. glossopharyngeus they would have associated with the most posterior trunk of the lateral group of the prootic ones in order to reach the most posterior part of the lateral electric field.

Possible ganglionic formations pertaining to the prootic electric nerve fibres must obviously have been situated in the vestibular division of the labyrinth cavity and, more exactly, in the ventral and medial parts of that division.

The dorsal electric field was supplied with arterial blood by branches from the postorbital superficial artery (*a. dsm*, text-figs. 44, 46, 47, 49, 51) and possibly also by the chief part of the artery which presumably ascended from the cavum cerebrale cranii through the canal *dx*. The lateral electric field received its arterial blood through the most distal branches of the facial artery (*a. am*, *a. iol*, text-figs. 44, 46, 47, 49) and through the most distal branches of the dorso-lateral superficial arteries (*a. sa*, *a.* sm_1, *a.* sm_2, *a. sp*, text-figs. 44, 46—49) and perhaps also, in its lateral part, through branches from the marginal artery. The dorsal electric field was drained by four veins (*v.* dsf_1, *v.* dsf_2, *v.* dsf_3, *v.* dsf_4, text-figs. 46, 50). The first one of these veins united with the posterior supraorbital vein and emptied into the orbital part of the v. capitis lateralis. The second one was a tributary to the supposed otical vein (*v. dsv*), and its blood was thus carried to the occipital vein sinus (*vs. oc*) and from this to the v. capitis lateralis. Of the third and fourth ones the former opened into the posterior corner of the occipital vein sinus and the latter into the myelonal veine 2; and their blood was thus also carried to the occipital vein sinus and from this to the v. capitis lateralis. The lateral electric field was drained by the distal branches of the dorso-lateral superficial veins 1—6 (*v.* ls_1—*v.* ls_6, text-figs. 46—51) and probably in its lateral parts also by branches of the marginal vein. The chief parts of its blood was thus brought to the v. capitis lateralis, the rest, on the contrary, probably to the v. marginalis. We thus find that, on account of their relations to the vessels, the electric fields must be considered to be superficial organs situated chiefiy beneath the corium.

The possibility is not quite out of question of course, that the organs described here as electric fields might have been sensory organs with a special function. But since it is very difficult to understand what this special function could have been, and since the organs in question undoubtedly have certain superficial resemblance to electric organs, especially to those in *Torpedo* (cf. DANIEL, 1922, fig. 115, p. 118; FRITSCH, G. 1890), I feel inclined to think that in reality they were electric organs, and because of that they have been referred to as electric fields throughout this work.

If this view is true, if the organs termed here the electric fields really were electric organs, it is obvious that they must have had their superficial parts, which were situated above the nerve canals, occupied by a thin layer of electric plates, which must have been arranged more or less parallel with the upper surface of the cephalic shield. Under the assumption that my opinion of their function is true, it is further clear that the electric fields, owing to their superficial position and relations to the skeleton, probably, unlike the electric organs of most fishes, could not have evolved from muscles but that they must have arisen either from the most basal part of the corium aponeurosis or from the tissue just beneath that or from both. Accordingly the Cephalaspids would in this respect be nearest comparable to *Malopterurus electricus* which, as is well known, has an electric organ which perhaps has been derived from the corium (cf. BALLOWITZ 1899, pp. 67—68).

Certain remarks on the trunk and the fins.

The trunk of the Spitsbergen Cephalaspids is very imperfectly known, since, as a rule, there is nothing preserved of it except the most anterior part of its exoskeleton that is coalesced with and forms part of the cephalic shield. This part of its exoskeleton was described in detail above in the general account given of the cephalic shield.

As is obvious from the interzonal part of the cephalic shield, the most anterior part of the trunk was with regard to its shape rather different in different forms. Thus in certain forms it was higher than broad or about as high as broad, while in others it was decidedly broader than high. Generally it was in transverse section more or less rounded triangular or pentagonal (text-fig. 79 D); but in certain cases it might perhaps have been rather oval.

The part of the trunk behind that just considered was in the Spitsbergens forms covered with scales which, as far as can be judged, must have been about as in the well preserved British *Cephalaspis*-species (cf. LANKESTER 1870, text-fig. 16, pl. 8, fig. 1; pl. 10, fig. 1; pl. 11, figs. 1, 2; WOODWARD 1891 a, pp. 177—178, text-figs. 21, 24; pl. 10; 1906 text-fig. 2; 1920, fig. 4; PATTEN 1903 c, text-figs. 5, 6, 10; pl. 1, figs. 1, 5; pl. 2, figs. 7—9).

Since, as we have seen, there is in the cephalic shield a part which, as far as can be judged, is homologous with the shoulder-girdle of fishes, it is obvious that the fin-like appendage which was situated in the pectoral sinus and which articulated against this shoulder-girdle-part of the cephalic shield is in reality a pectoral fin. Unfortunately nothing is known of the pectoral fin in the Spitsbergens forms; but in the forms from Britain it is in many cases well preserved and found to be covered with thin scales (cf. LANKESTER 1870, p. 41; pl. 8, fig. 1; pl. 10, fig. 1; pl. 11, figs. 1, 2; WOODWARD, 1891 a, pl. 10, fig. 1; 1920, fig. 4; PATTEN 1903 c, text-figs. 5, 6; pl. 1, figs. 1, 3; pl. 2, fig. 8; GOODRICH 1910, text-fig. 173, very good figure; etc.). Nothing of its internal skeleton is known. As pointed out by LANKESTER, it is very remarkable that it exihibits no traces of fin-rays.

Of the unpaired fins nothing is preserved in the Spitsbergen Cephalaspids. On the other hand these fins are in certain cases well preserved in the British forms (cf. LANKESTER 1870, text-fig. 16, pl. 10, figs. 1, 4; pl. 11, figs. 1—3; WOODWARD 1891 a, text-fig. 24; 1906, text-fig. 2; 1920, fig. 4; PATTEN 1903c, text-figs. 5, 6; GOODRICH 1909, text-fig. 173; JAEKEL 1911, text-fig. 21; STROMER 1912). These fins are all provided with distinct rays.

The pronephros.

Immediately dorso-laterally to the oesophagus foramen or its homologue, in those cases when the oesophagus foramen and the truncus arteriosus foramina are united into a common one, there issues, as we have seen (cf. pp. 148—149 above), from the posterior surface of the postbranchial wall a paired very thin lamella, *p. nl* (text-figs. 9, 10, 33—35; section series F, nos. 8—28) in a posterior direction. More exactly, this lamella, *p. nl*, issues from the postbranchial wall along a dorso-ventrally and somewhat laterally running line, and owing to this it is somewhat inclined towards the median line with its upper part. How far it reached dorsally cannot be decided with full certainty, since in the materal available it is not found completely preserved. It is, however, very likely that it did not meet its fellow of the other side dorsally. In its posterior part it was, at least in certain cases, curved somewhat towards the median line, as is well shown by text-fig. 9 and section series F, nos. 8—28.

Together with its fellow of the opposite side, the lamella *p. nl* just described encloses from each lateral side a space lettered *p. nephr* in the figures (text-figs. 9, 10, 33—35; section series F, nos. 8—28), which was bounded anteriorly by the posterior surface of the postbranchial wall, but which on the other hand was open ventrally, posteriorly and very likely also dorsally. This space is in its anterior part subdivided into a right and a left part by means of a short sagittal lamella (*p. nm*, text-figs. 9, 10, 33—35; section series F, nos. 8—20) which issues from the posterior surface of the postbranchial wall in a posterior direction. But since this unpaired lamella, at least in the cases in which it could be studied in detail, is not situated exactly in the median line but lies somewhat on the right side of this, the right part of the space *pr. nephr* is less broad than the left one. Into each part opens a fine canal (*a. prn*) which comes from in front from the cavity for the arteria branchialis efferens communis (*a. eff. com*). This fine canal obviously transmitted an artery.

What is known otherwise of the anatomy of the Cephalaspids makes it quite clear that the space *pr. nephr* is situated immediately beneath the aorta and above the oesophagus and the pericard and that it thus had a position which alone makes it very probable that it lodged the pronephros, which, as we know, has corresponding relations to the aorta, the oesophagus and the pericard. Now since the paired lamella *p. nl* on its medial side has been found to have a number of rather fine, chiefly vertical, grooves separated by low ridges (section series F, nos. 8—17), and since similar grooves and ridges are present on the part of the posterior surface of the postbranchial wall that forms the anterior boundary of the space *pr. nephr*, it seems to me quite certain that this space really lodged the pronephros, for the said grooves and ridges can only have been caused by an organ consisting of tubuli like the pronephros.

In view of the relative small number of grooves and ridges it is evident that the number of pronephros tubuli was rather small. Since the grooves and ridges do not run quite regularly in a dorso-ventral direction, it seems highly probable that the pronephros tubuli had a somewhat winding course upwards from the pericard, into which they probable opened.

As we see we are forced to the conclusion that in the adult Cephalaspids there still persisted a functionary pronephros consisting of a few tubuli situated exactly in the normal way. We thus find that the Cephalaspids also in this respect were very lowly organized vertebrates nearest comparable to the Cyclostomes (cf. GOODRICH 1909, pp. 43—45, etc.), and among these especially to the Petromyzontids.

To elucidate further how similar the conditions with regard to the pronephros must have been in Cephalaspids and *Petromyzon*-larvae I wish to call special attention to text-fig. 99 below which is a copy after pl. 11 in CORI's paper in 1906 on the vascular system of *Ammocoetes*, but which in addition shows the pronephros in its position in relation to the branchial basket, the heart and the main vessels.

Description of genera and species.

Genus **Cephalaspis** Agassiz.

Syn. *Eucephalaspis*, Lankester, E. R., 1870, p. 43.

Zenaspis, Lankester, E. R., 1870, p. 43.

How the genus *Cephalaspis* got its present definition and other facts with regard to its history have been dealt with in the general historical review of the Cephalaspids given in this monograph (pp. 1, 2 above).

From the upper Silurian (Downtonian) and the lower Devonian deposits of Spitsbergen there are at present known not less than 20 *Cephalaspis*-species, all of which seem to be new. It is, highly probable however, that the total number of *Cephalaspis*-species in these deposits is still greater, for there are several fragmentary remains among the material available which seem not to pertain to any of the species described, but which on the other hand are too imperfect to enable the establishing of new species for them.

Among the species of the genus now described from Spitsbergen 11 are from the upper Silurian (Downtonian) and 9 from the lower Devonian. With those species that have been described from other localities than Spitsbergen included, the total number of *Cephalaspis*-species known at present thus exceeds 30.

Since the total number of *Cephalaspis*-species discovered in the upper Silurian is about 14 it is perfectly obvious that the genus *Cephalaspis*, as now defined, attained a great flourishing already in the Silurian, and that *Cephalaspis*-species must occur still lower in the Silurian than is known hitherto.

Like Lankester in 1870 (p. 43), I am of the opinion that the species generally known as *C. murchisoni* represents a genus of its own, a genus for which the name *Hemicyclaspis* introduced by Lankester is to be used. No further subdivision of the genus *Cephalaspis* is at present possible.

The characters distinguishing the various species are: the general shape and proportions of the cephalic shield, the configuration of the rostral margin, the shape, direction and denticulation of the cornua, the shape and size of the pectoral sinus, the shape and backward extension of the interzonal part, the size and position of the orbital openings, the shape and extension of the electric fields, and finally the ornamentation, which, however, in certain forms seems to show a rather considerable variation and therefore probably is of less importance than the other characters.

Owing to the fact that most of the material is very imperfectly preserved, and in addition often to a certain degree distorted, the determinations as to species are in many cases very difficult, and it should therefore be pointed out here that in the future, when they become known more in detail, certain among the new species now established may appear to the identical with each other, while others perhaps may reveal themselves to be too widely defined.

With the extended knowledge obtained by the investigation of the Spitsbergen material the definition of the genus given by WOODWARD in 1891 (1891 a, pp. 177—178) can now be completed in certain respects and would be as follows. Cephalic shield more or less distinctly triangular in outline. Cornua well developed, directed posteriorly or postero-laterally and, as a rule, not exceeding the shield in length, but always projecting backwards beyond the interzonal part. In certain species the rostral part of the shield extended into a rostral process. Pectoral sinus generally distinct. Interzonal part of varying length, but not exceeding the cornua in length. One unpaired dorsal and one paired lateral electric field. The common canal for the two most anterior ones of the nerves to the lateral electric field dividing into its two chief branches already close antero-laterally to the orbit and the canal for n. trigeminus proper passing in the interspace between these two branches, though in a deeper level than these. The canal for the dorso-lateral superficial vein 3 leading to and opening into the postero-dorso-medial corner of the orbit. Body more or less distinctly triangular in transverse section. Flank-scales in three series, the upper series of each side meeting in the mesial line above, the middle series deepest, and the lowermost forming an infero-lateral fringe, often serrated; ventral scales small, arranged in *V*-shaped transverse rows equal in number to the series of flank-scales.

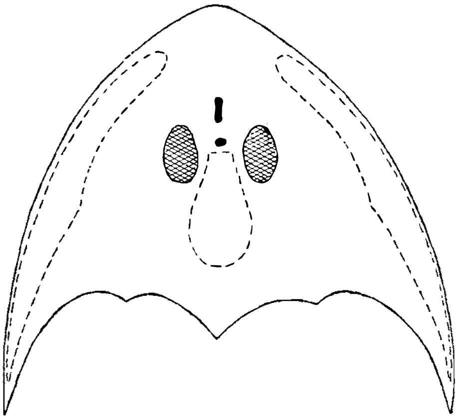
1. *Cephalaspis watneliei* n. sp.

(Pl. 1, figs. 1, 2; text-fig. 53).

The species is represented merely by a single cephalic shield (specimen no. 1), which is slightly flattened and in part fractured and distorted by pressure after the embedding in the rock.

The shield measures in length from the rostral to the posterior angle 4,2 cm., while its breadth between the posterior ends of the cornua (the maximum breadth) is about 6,2 cm., and the breadth at the posterior angle about 6,1 cm. The height amounts to about 0,8 cm., but probably was originally greater. The interzonal part of the shield is about 2,6 cm. broad, and accordingly its breadth is contained about $2^1/3$ times in the maximum breadth. As is evident from these measurements, the shield is from an individual of rather small size.

The rostral angle is distinctly developed. The cornua, which point backwards and slightly laterally, are rather broad and flat in dorsi-ventral



Text-fig. 53. *Cephalaspis watneliei* n. sp. Restoration of the cephalic shield. 1/1.

direction, and, as far as can be seen, they have no pectoral angle and no denticles. The pectoral sinus is rather wide and strikingly shallow. The interzonal part is rather broad and very short, almost as in *Hemicyclaspis murchisoni*, and has a distinct posterior angle. Whether a dorsal spine was present or not, it is not possible to decide with full certainty, but it seems improbable that this was the case. The orbits are rather large in relation to the size of the cephalic shield, and what is further characteristic of them is that their longitudinal axes diverge only very slightly from each other forwards. The dorsal electric field has its broadest places situated in the posterior half. The lateral electric field extends far backwards on the cornu of its side, probably almost to the posterior end of that, gradually decreasing in breadth posteriorly. Several of the nerve canals to the left lateral electric field are distinctly seem.

No certain traces of tuberculation are to be discovered along the anterior and lateral margins. Otherwise nothing can be said concerning the character of the ornamentation. The external parts of the exoskeleton are subdivided into numerous rather small polygonal areas.

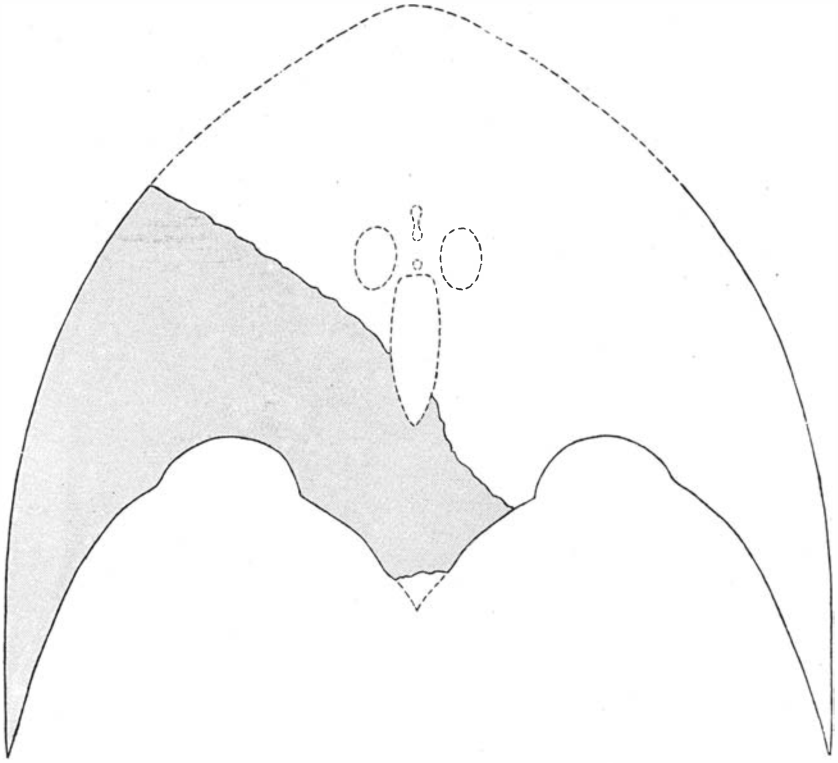
Remarks. — The cephalic shield described here, though resembling in certain respects that of *Cephalaspis lyelli*, cannot be referred to that species, but must represent a new one, which I have named *C. watneliei* after G. WATNELIE, Lecturer, Sarpsborg Secondary School, who took part in the Norwegian expeditions in 1909—1912 for the exploration of the Old Red deposits in Spitsbergen. The species is characterized by the general shape of the shield, the length and shape of the cornua, the shallow pectoral sinus, the very inconsiderable length of the interzonal part, the large orbital openings, and the peculiar shape of the dorsal electric field.

Geological series, horizon and locality. — Lowest part of the Wood Bay series (lower Devonian), W. of the Hoffnung glacier. Collected by ADOLF HOEL in 1912.

2. *Cephalaspis borealis* n. sp.

(Pl. 1, fig. 3, text-fig. 54).

The material available of this species consists only of a posterolateral fragment of a cephalic shield (specimen no. 2). This fragment, however, enables me to arrive at a quite definite opinion concerning the shape of the posterior part of the shield.



Textfig. 54. *Cephalaspis borealis.* n. sp. Shaded part present. Other parts restored. Slightly larger than 2/3 of the nat. size.

The length of the shield is not known. The breadth somewhat anteriorly to the posterior angle is about 16 cm., amounting to 17 cm. (maximum breadth) between the posterior ends of the cornua. The height in the interzonal part is about 2 cm. The interzonal part is about 4,9 cm. broad between the lateral angles, and its breadth is thus contained about 3½ times in the maximum breadth of the shield. As is obvious from these measurements, the shield is from a large animal.

The cornua, which issue in a posterior and slightly lateral direction, are long, broad and strong and much flattened from the dorsal to the ventral side. They have a pectoral angle on the medial side, but whether they were provided with denticles or not cannot be decided with certainty. The pectoral sinus, which is broad and rather deep, is well defined. The interzonal part is narrow and rather long, and it was probably provided with a very pronounced posterior angle. On its dorsal surface there is an obtuse median ridge running from the posterior angle forwards towards the posterior end of the dorsal electric field. This field appears to have been rather narrow, with an at least somewhat pointed posterior end. Its anterior parts are not preserved. The shape and extent of the lateral electric field are entirely unknown.

The left half of the postbranchial wall is to be seen in the specimen, though, owing to its thinness, it is badly preserved. In the median part it shows traces of a foramen, certainly the foramen for the oesophagus. Otherwise it is to badly preserved to exhibit any details.

The endoskeletal bone on the dorsal side of the shield is thin, a fact which seems to be due to the circumstance that in most places hardly anything more than the inner laminated layer of the ordinary three is present. (Only in one place I can find distinct remains of the middle layer, while the superficial layer seems to be entirely absent).

Remarks. — Though very fragmentarily preserved, the cephalic shield described here nevertheless shows so many characteristic features that it seems beyond question that it represents a new species. It is characterized especially by its long, strong cornua, its distinctly defined, deep pectoral sinus and the narrow rather long interzonal part.

Geological series and locality. — Wood Bay series (lower Devonian). Wood Bay. Probably collected by G. WATNELIE in 1910.

3. *Cephalaspis oblongus* n. sp.

(Pl. 2, fig. 2; text-fig. 55).

This species is established for the left half of a much flattened shield (specimen no. 3). This shield, the outlines of which can be easily restored, measure, about 12,4 cm. in lenght from the rostral end to the line between the posterior ends of the cornua. Its length from the rostral end to the posterior angle, on the contrary, cannot be ascertained, since the interzonal part is imperfectly preserved. The breadth between the posterior ends of the cornua amounts to 9,8 cm., and the maximum breadth, which is situated somewhat more anteriorly, is about 10,7 cm. The interzonal part of the shield is about 8,3 cm. broad, and its breadth is thus contained more than three times in the maximum breadth[1].

As is shown by these figures, the cephalic shield here in question is from a comparatively large animal.

With regard to the general shape the cephalic shield is even in its present, much flattened condition distinctly longer and narrower than in the two species described above. The rostral border is imperfect anteriorly, and it is therefore difficult to say how the conditions were there, whether there was a rostral angle or not. The cornua, which are directed almost straight backwards, are broad and long and much flattened in a dorsi-ventral direction. They have no distinct pectoral

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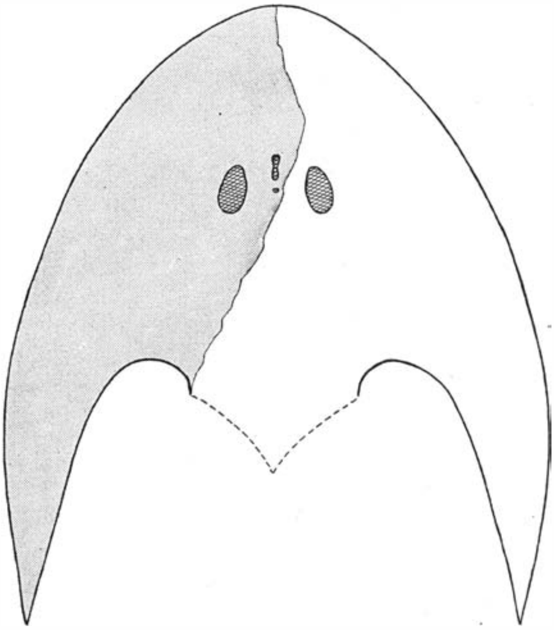
[1] All these measurements refer to the shield in its present very flattened condition. And it is therefore very probable that the shield in its original condition was still more narrow in relation to its breadth.

angle and seem also to be devoid of denticles. The pectoral sinus is well developed. The interzonal part, which is imperfectly preserved, appears to be narrow. Concerning its length, on the contrary, only so much can be said that it was not as short as in *C. watneliei.* The orbits are rather small and oval, almost twice as long as they are broad. They are situated in such a way that their longitudinal axes converge forwards. The nasal aperture, with its normal shape, and the pinela foramen are clearly distinguishable. The shape and extent of the electric fields remain unknown, but it is very probable that the lateral electric field reached far backwards on the cornu of its side.


Text-fig. 55. *Cephalaspis oblongus* n. sp. Restoration of the Cephalic shield. The parts of the shield preserved denoted by shading. 2/3.

The endoskeletal bone of the shield is imperfectly preserved, with regard to structure, but from what there remains of it it seems to have consisted chiefly of the basal, laminated layer, quite as in *C. borealis.*

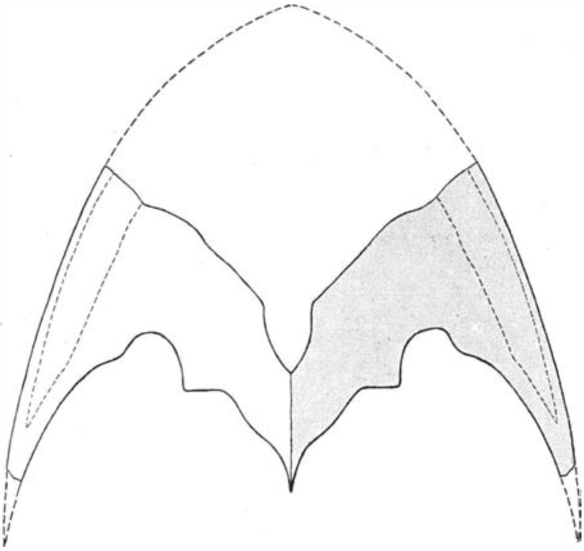
Remarks. — The cephalic shield described here obviously resembles in certain respects that of *C. borealis*, but differs from that very distinctly in the general shape and proportions, and in the shape and direction of the cornua. It undoubtedly represents a new species, a species for which I propose the name *oblongus*, on account of the relatively narrow appearance of the shield as a whole.

Geological series and locality. — Wood Bay series (lower Devonian), 150—300 m. above the sea on the north side of a valley in the vicinity of Mt. Halvdan. Collected by ADOLF HOEL in 1912.

4. *Cephalaspis acuticornis* n. sp.

(Pl. 2, fig. 4; text-fig. 56).

This species is based on a single postero-lateral part of a cephalic shield which is much weathered and abraded (specimen no. 55). That part, however, makes it possible to ascertain with certainty the shape of about as much as the posterior half of the shield.



Text-fig. 56. *Cephalaspis acuticornis* n. sp. Restoration of the cephalic shield. The part of the shield present denoted by shading. 2/3.

The shield measures in breadth at the anterior ends of the pectoral sinus 7 or 8 cm., slightly anteriorly to the posterior ends of the cornua about 9—10 cm., and at at the very posterior ends of the cornua probably slightly more (maximum breadth). The height in the interzonal part is, as far as can be judged, rather considerable, perhaps even as much as about 4 cm. The breadth of the interzonal part, taken between the lateral angles, amounts to 3,5 or 4 cm., and it is thus somewhat more than a third of the maximum breadth.

The configuration of the anterior border of the shield is not known. The cornua, which are directed postero-laterally, are well developed, but shorter than in *C. borealis* and *C. oblongus*. They are flattened in a dorsi-ventral direction and have a very distinct pectoral angle. Behind this angle their medial margin is rather much concavated, a condition which causes them to taper rapidly backwards and to get rather slender in their distal parts. Their medial margin lacks denticles. The pectoral sinus is narrow, but deep and well defined. The interzonal part is rather broad and long, in fact almost as long as the cornua, and has on the dorsal side a very strong median longitudinal ridge (text-fig. 56; pl. 2, fig. 4) which most posteriorly is produced into a small dorsal spine, rather strongly inclined backwards. The dorsal electric field is not preserved, but it seems probable that it was rather pointed posteriorly. The lateral electric field extends backwards on the cornu of its side, but not to the very posterior end of that, and it gets rapidly narrower most posteriorly.

The exoskeletal bone of the cephalic shield in this species certainly had the normal structure, as described by Huxley in 1858; and the ornamentation probably consisted of small numerous tubercles. More details concerning the ornamentation, however, cannot be made out. Concerning the exoskeleton it is further worthy of notice that it had its outer parts subdivided into numerous, rather small polygonal areas. (Pl. 2, fig. 4).

Remarks. — The specimen described here is very distinctly separated from the other Spitsbergen species and seems also to be very different from all other species known. I have therefore not hesitated in establishing for it a new species, a species which, because of the pointed shape of the cornua I have named *acuticornis*.

Geological series and locality. — Wood Bay series (lower Devonian). Ridge between the Arla and Serla glaciers. Collected by O. HOLTEDAHL in 1909.

5. *Cephalaspis isachseni* n. sp.

(Pl. 3; text-fig. 57).

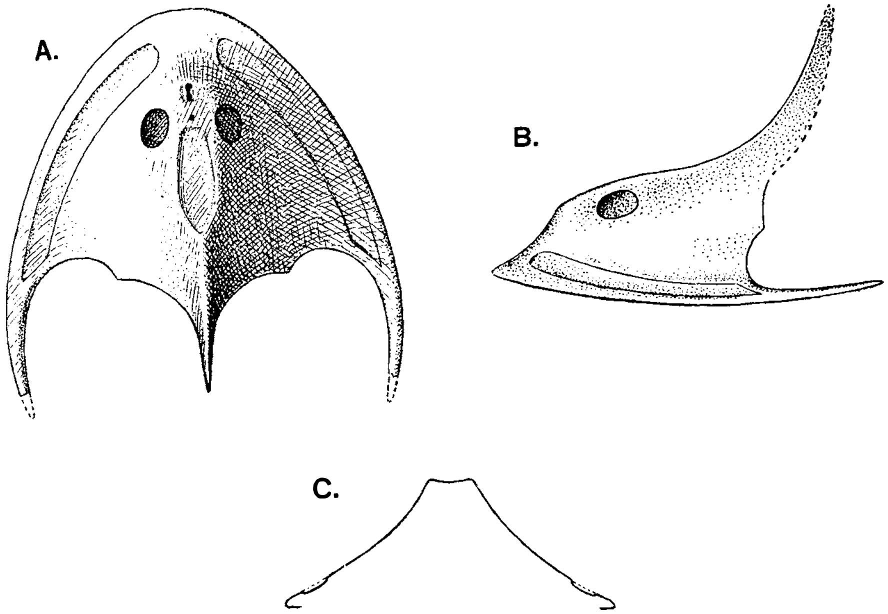
This species is based on a complete cephalic shield (specimen no. 4). With hesitation fragments of a second cephalic shield (specimen no. 5) occurring in the same sample as the type specimen are in addition referred to it. Where nothing else is stated the description is based solely on the type (specimen no. 4).

The length from the rostral margin to the posterior preserved end of the dorsal spine is about 5,1 cm. The breadth at the posterior ends of the cornua amounts to about 4,6 cm., and 1 cm. farther forwards to about 5,2 cm., this latter being the maximum breadth. The maximum breadth thus only slightly exceeds the length. The height, measured about 0,8 cm. behind the pineal opening, is not less than about 2 cm. The interzonal part is about 2,3 cm. broad (at the posterior ends of the pectoral sinus), its breadth thus being almost exactly one half of the breadth between the posterior ends of the cornua.

As is obvious from the measurements given, the shield described here under the name of *C. isachseni* is from a rather small animal.

The rostral margin has no angle and seems to have been rather obtuse. The cornua, which issue backwards and are distinctly curved inwards, are rather long and very slender. At least in their distal halves they are almost circular in transverse section and not dorsi-ventrally flattened as in most other species. They seem to lack denticles. The pectoral sinus is broad but rather shallow. The interzonal part is short and broad. Concerning the interzonal part it is further to be mentioned that it is provided with a high and strong spine (*dsp*, text-fig. 57; pl. 3, fig. 3) which, however, is imperfectly preserved posteriorly, so that its breadth in antero-caudal direction, its shape posteriorly, and its exact inclination backwards cannot be ascertained. Anteriorly the base of this spine reached to the posterior end of the dorsal electric field.

The orbits are rather large and are almost as broad as they are long. Their longitudinal axes are almost parallel, or in any case they converge only very slightly forwards. The pineal opening is distinctly seen in its normal place. The nasal opening is injured, so that it does not show its original shape.



Text-fig. 57. *Cephalaspis isachseni* n. sp. Cephalic shield. A, in dorsal view; B, in lateral view, and C, in transverse section approximately 0,8 cm. behind the pineal foramen. Approximately nat. zise.

The dorsal electric field is a rather deep and narrow depression, which seems to have had its broadest part situated behind the middle of its length. And, as far as can be seen, its posterior end was rather pointed. The lateral electric field has an approximately equal breadth throughout its length, and a thing that is especially characteristic of it is that it reaches backwards only a very short distance on the cornu of its side, in fact not more than about a fourth of the length of the cornu. Several branches of the nerve canals leading to the left lateral electric field are distinctly preserved and well displayed (pl. 3, fig. 2, 3).

Of the endoskeleton only certain parts of the ventral wall of the cranial cavity and of the postbranchial wall are to be seen, and it is obvious that both these structures were rather thick. The latter of them is perforated by a median unpaired large foramen, which lies rather high and which therefore must be the oesophagus foramen. Finally it may be mentioned that in this wall remains of the canal for the arteria subclavia can be seen.

The exoskeletal bone of the cephalic shield is thick and well developed and is on the outside ornamented with numerous rather strong scattered tubercles. In pl. 3 fig. 3 these tubercles are seen as small whiteish spots in those places on which the inner and middle layers of the bone have split off, e. g. laterally and anteriorly to the orbital opening between this and the lateral electric field. Similar tubercles also occur on the cornua. Worthy of notice in this connection is further the fact that the external parts of the exoskeleton show no indications whatever of polygonal areas.

Remarks. — This species, which in certain respects is somewhat suggestive of *C. lyelli*, is very well characterized especially by the slender shape of its cornua and the very strong and high dorsal spine. It has been named after major G. ISACHSEN, the initiater of the Norwegian exploration of Spitsbergen and the leader of the expeditions 1906—1907 and 1909—1910 during which a considerable part of the material described in this monograph was brought together. The specimen (no. 5) referred to this species with hesitation is too imperfectly preserved to be determined with certainty. As far as is known, however, it seems to agree with the holotype.

Geological series horizon and locality. — Lowest part of the Wood Bay series (lower Devonian), W. of the Hoffnung glacier. Collected by ADOLF HOEL in 1912.

6. *Cephalaspis laticornis.*

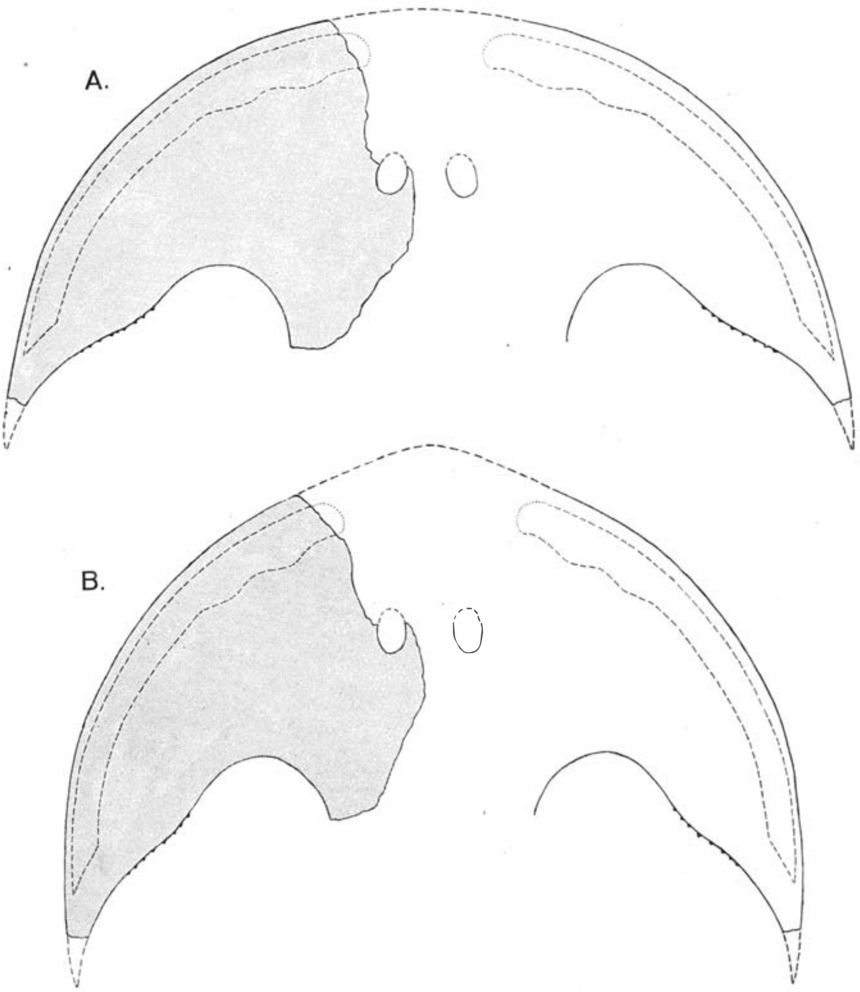
(Pl. 4, fig. 1; text-fig. 58).

This species is established for a fragment of the right side of a cephalic shield (specimen no. 6).

On account of the fragmentary state of that cephalic shield no certain measurements can be given either of its length or breadth or of its height. What is preserved of it is seen in natural size in pl. 4, fig. 1. And, as is obvious, it is from a large animal.

As far as can be judged, the general shape of the shield may have been either about as in text-fig. 58 A or approximately as in text-fig. 58 B. But in view of certain conditions with regard to the dorsal electric field the former of these two alternative seems, however, to be the most probably one. The cornua are very broad and much flattened in dorsi-ventral direction, with the medial margin somewhat concave in the posterior half. Concerning their medial margin it should further be pointed out that this has a very obtuse pectoral angle, and that this and the stretch of the medial margin close posteriorly to it are provided with a few short denticles. The pectoral sinus is not so very broad but deep and well defined. The orbits are rather small in relation to the size of the shield. The dorsal electric field is not preserved. The lateral electric field, which is strikingly narrow in the posterior larger part of its length, extends rather far backwards on the cornu of its side, but not as far as to the posterior end of that.

Concerning the structure of the exoskeleton it deserves to be pointed out that the superficial and middle layers both seem to have been thin. At least the medial margin and ventral rim seem to have



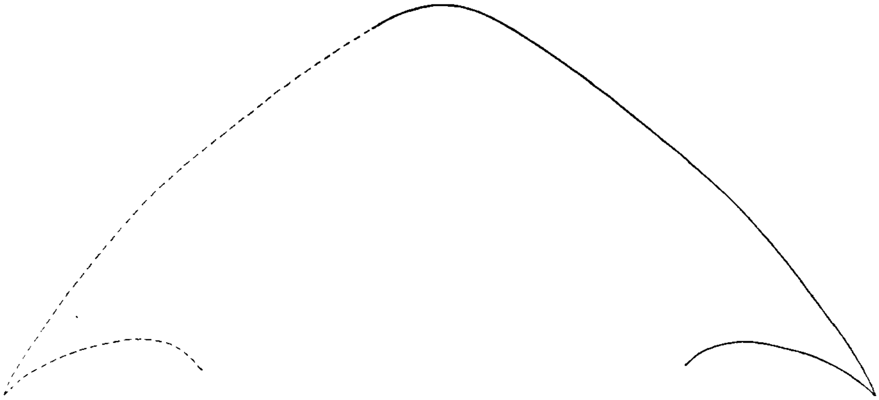
Text-fig. 58. *Cephalaspis laticornis* n. sp. Possible outlines of the cephalic shield. The parts present of the shield denoted by shading. Approximately 2/3 of nat. size.

had no tuberculations buth are smooth. Otherwise nothing is known with certainty concerning the ornamentation.

The external parts of the exoskeleton are subdivided into numerous small polygonal areas.

Remarks. — The species described here is very distinctly characterized from other species by its very broad, peculiarly shaped cornua, and on account of this I have named it *laticornis*.

Geological series and locality. — Wood Bay series (lower Devonian), Wood Bay. Probably collected by G. WATNELIE in 1910.



Text-fig. 59. *Cephalaspis brevicornis* n. sp. Probable outlinec of cephalic shield. Sketch based on specimen no. 8. Approximately 1/3 of the nat. size.

7. *Cephalapsis brevicornis* n. sp.

(Pl. 4, fig. 2; pl. 5, figs. 1, 2; pl. 12; text-fig. 59).

As far as can be judged, this species is represented by fragments of four cephalic shields (specimen nos. 7, 8, 13, 56) among which the most complete one (no. 8, pl, 5, fig. 1) has been chosen as a holotype.

All the fragments known are from wery large individuals. The holotype has in its present imperfect state of preservation a length of about 15 cm. from the rostral end to the present posterior border of the interzonal part. The breadth between the posterior ends of the cornua probably amounted to about 30 cm., and thus the breadth was probably approximately twice as great as the length. One of the other specimens (no. 13; pl. 12) was probably still larger.

The rostral margin seems to form an angle, though this angle is very obtuse and indistinct. The cornua, which are broad and strikingly short and which in addition are rather flat in a dorsi-ventral direction, issue much more in a lateral direction than in the six species described above. They decrease continuously and rather rapidly in width distally and seem to be without pectoral angle and denticles on their medial border. The pectoral sinus is shallow and broad, not distinctly defined. The interzonal part is also broad, but is so imperfectly preserved that nothing can be etablished either as to its shape otherwise or as to its backward extension. The orbital openings and the dorsal electric field are not preserved. The lateral electric field, which extends backwards on the cornu of its side — although not so far as in *C. watneliei* — is rather narrow.

The exoskeletal bone of the shield is not very thick but seems nevertheless to be composed of the usual three layers. The ornament consists, along the lateral borders, of numerous very coarse, flat tubercules (pl. 5; fig. 2; pl. 12), otherwise of numerous very small tubercles (pl. 4, fig. 2). Whether the exoskeleton was subdivided externally into polygonal areas cannot be decided with certainty.

Remarks. — The four specimens described here agree with each other with regard to the shape of the cornua, the ornamentation, and, as far as can be judged, also with regard to the general shape of the shield. I therefore think that they must belong to one and the same species. This species is well characterized from other species by its very considerable size, by the general shape of the cephalic shield, by the ornamentation and by the short robust cornua.

Geological series and localities. — All the specimens referred to *C. brevicornis* are from the Wood Bay series (lower Devonian). Specimens no. 7 and no. 13 have been found at Wood Bay. Specimen no. 8 is from the inland East of Kings Bay, and specimen no. 56 from a point near Mt. Lyktan, Dickson Bay. Specimen no. 8 was collected by O. HOLTEDAHL in 1909 and specimen no. 56 by A. HEINTZ in 1925. The two remaining specimens have probably been collected by G. WATNELIE in 1910.

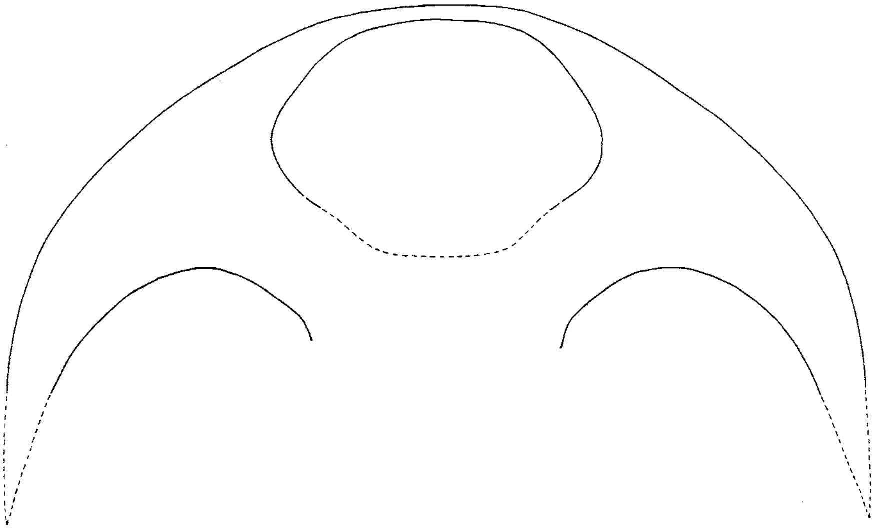
8. *Cephalaspis lata* n. sp.

(Pl. 6, fig. 1; pl. 7; text-fig. 60).

This species is based on two fragmentary cephalic shields (specimen no. 9 and specimen no. 10), both of which are preserved in such a way that they display the ventral side rather completely.

One of these cephalic shields (the type-specimen, no. 9; pl. 7) is from a very large individual. The length from the rostral border to the posterior end of the preserved portion of the interzonal part cannot be ascertained with full certainty, but may be estimated at about 10—12 cm., whereas the breadth between the posterior ends of the cornua was not less than about 28 or 30 cm. The second cephalic shield (specimen no. 10; pl. 6, fig. 1) is much smaller, its length probably beeng not more than 6—7 cm. and its breadth between the posterior ends of the cornua about 17 cm. As is obvious from these measurements, the cephalic shield of this species is especially characterized by its considerable breadth, which is almost tree times as great as the length.

The rostral end of the shield is rounded and very obtuse without traces of a rostral angle. The cornua, which issue in a postero-lateral direction, are long broad and flat and not straight but somewhat curved in a medial direction. Their medial border seems to lack both a pectoral angle and denticles. The pectoral sinus is broad and deep, but not very distinctly defined. The interzonal part was probably very narrow, but it



Text-fig. 60. *Cephalaspis lata* n. sp.
Restoration of the cephalic shield, from the ventral side. After specimen no. 9. 1/3.

is imperfectly preserved, so that nothing certain can be established as to its length. Orbits and electric fields not known.

The ventral opening of the oralo-branchial chamber, the oralo-branchial fenestra, is partly shown in both specimens. It is considerably broader than it is long.

In the smaller (no. 10) of the two shields the exoskeletal bone is almost entirely weathered away. In the larger one, on the contrary, it is partly well preserved and appears to be rather thick and to be composed of the usual three layers. The superficial one of these layers forms, at least on the ventral side of the shield, a continuous quite smooth covering on the middle one, and as usually, when it is well developed, it is perforated by numerous pores. Otherwise it is worthy of notice here that the exoskeleton in its external parts is subdivided into numerous polygonal areas.

Remarks. — The two cephalic shields described here agree, as far as they are known, in all essential characters, and I feel therefore rather convinced that they pertain to the same species. The considerable breadth in proportion to the length and the shape and direction of the cornua differentiate them quite distinctly from those of other known species, and a new species has therefore been established for them.

Geological series and localities. — Wood Bay series (lower Devonian). The largest shield (no. 9) is from Mt. Högkulla on the Reindeer Peninsula; the other (no. 10) has been found W. of the Hoffnung Glacier. The first mentioned one was collected by O. HOLTEDAHL in 1909, the other one by ADOLF HOEL in 1912.

9. *Cephalaspis höegi* n. sp.

(Pls. 8—10; text-figs. 61—63).

The species *C. höegi* is based on an imperfectly preserved cephalic shield, with considerable portions of the cornua and the interzonal part missing (specimen no. 11, pl. 8). Besides that cephalic shield two other imperfect ones (specimens nos. 12 and 115) and a fragment of a cornu (no. 114) may perhaps also belong to this species.

All of the shields mentioned are from large or rather large animals. Thus the type shield (no. 11) attained a length[1] of at least 10—12 cm., whereas its breadth at the proximal parts of the cornua is about 18,5 cm. And one of the other shields (no. 12) is even somewhat larger.

Unfortunately all the shields are in such an imperfect state of preservation that it is difficult to compare them in detail with each other with regard to proportions and configuration. And because of that I have found it most convenient to describe each one of them separately.

We first deal with the type shield (no. 11, text-fig. 61; pl. 8). As is evident from the measurements given, that shield is considerably broader than it is long. Its rostral margin is obtusely rounded without any trace of a rostral angle. The cornua, which issue in a postero-lateral direction, are, at least in their proximal parts, broad and flat, their length and shape otherwise being unknown. The pectoral sinus was probably well developed and broad. The interzonal part, though very imperfectly preserved, seems to have been comparatively narrow, its breadth perhaps being contained about three times in the breadth of the shield at the anterior end on the pectoral sinus. The orbits are rather large and appear to be lined by a thin orbital layer of perichondral bone. The extension of the orbits postero-ventro-medially shows beyond question that a myodome (*my*, pl. 8) was present, quite as in the Downtonian species. The nasal opening has its normal shape and the pineal opening is small; and both these openings are situated strickingly far back in relation to the orbits. The dorsal electric field, which is imperfectly preserved, seems to have been rather broad even in its anterior end. The lateral electric field is broader anteriorly than posteriorly, where it is rather narrow, at least in proportion to the considerable breadth of the proximal part of the cornu. Its medial margin exhibits certain small convexities and concavities in its anterior part. The canal for the most anterior electric nerve is partly preserved on the right side (sel_1, pl. 8),

Most posteriorly in the shield, wich is displayed from the ventral side, there are to be observed certain traces of the postbranchial wall (*p. brw*, pl. 8).

The exoskeleton consisted of the usual three layers, but the superficial and middle layers are thin. At least along the lateral

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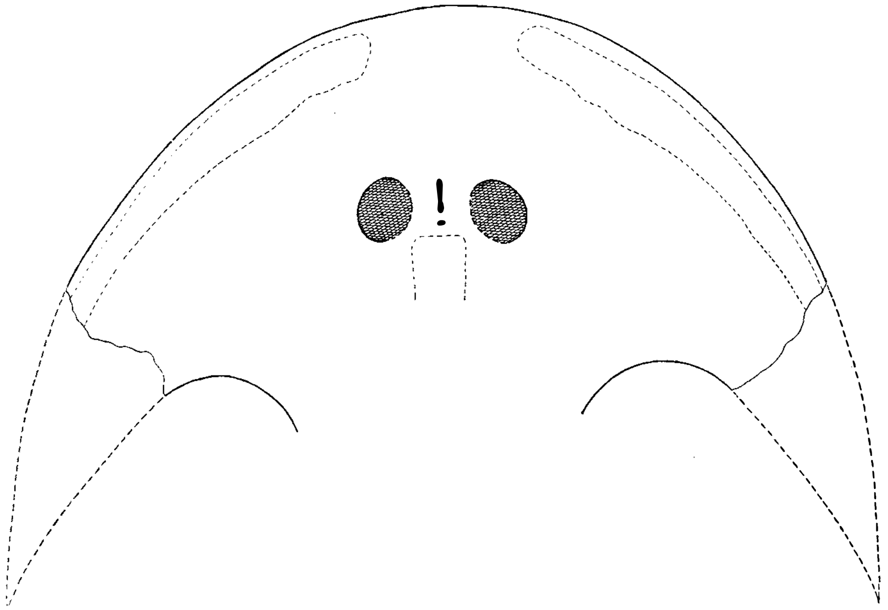
[1] From the rostral margin to the posterior end of the interzonal part.



Text-fig. 61. *Cephalaspis höegi* n. sp. Outlines of the cephalic shield of the type. Somewhat more than 1/2 of the nat. size.

borders and on the ventral rim the superficial layer seems to have formed a continuous covering of the middle layer and to have been without tuberculations, but on the dorsal side of the shield it is rather likely that it was provided with small rather numerous tubercles. In this connection it deserves also to be mentioned that the external parts of the exoskeleton are subdivided into numerous, small polygonal areas.

Turning to the other shields which have been assigned to the species with some doubt, we find that the biggest one of these (no. 12) is of a certain interest from an anatomical point of view, as it is one of the few Devonian shields, that exhibits somewhat well-preserved parts of the endoskeleton and the internal structures.

Unfortunately that shield (pls. 9, 10) is very imperfectly preserved, its dorsal part being entirely abraded and both its cornua broken off and lost.

Concerning the general shape of this shield it is only to be noticed that, as far as it is known, it seems to be most nearly like that of the type shield. And it is also probable that the cornua were broad, as in that. The exoskeleton of the dorsal side is not preserved. That on the lower side is rather thick and strong and composed of the usual three layers. At least on the ventral side and along the lateral borders the superficial one of the three layers is continuous and, at least most anteriorly, provided with rather low tubercles. Otherwise nothing is known concerning the ornamentation. As in the type, the external parts of the exoskeleton are subdivided into polygonal areas.

Of perichondral bone-layers we find in the specimen traces of the external one that lined the oralo-branchial chamber, the postbranchial wall and the endoskeletal shoulder-girdle and in addition also traces of the one that lined the marginal vein sinus. And owing to the occurrence of these traces of perichondral bone-layers, which lie in their original position we are able, to obtain a rather good idea of the structure of the oralo-branchial chamber and the postbranchial wall as well as of the marginal vein sinus and the endoskeletal shoulder-girdle. But attention must be called to the fact that the perichondral bone-layers are all very thin and that the external one lining the oralo-branchial chamber is present only on the most ventral parts of the walls of that chamber.

The oralo-branchial chamber was in its ventral parts certainly broader than it was long. Most ventrally, where the external perichondral bone-layer is found, it exhibits distinct traces of the ventral parts of certain branchial fossae and in addition traces of certain of the canals for the ventral transversal superficial veins (v_6—v_8, pls. 9, 10).

The postbranchial wall (*p. brw*, pls. 9, 10), which has the posterior side exposed for examination, is, as is asual in the *Cephalaspis*-species perforated by a big median foramen for the oesophagus and truncus arteriosus (*oes*, *tr*). Postero-ventrally to that foramen there is to be seen the small opening of the paired canal *fy* for the v. longitudinalis superficialis ventralis, and still more laterally and somewhat dorsally certain of the posterior openings for the posterior canals for ventral transversal superficial veins. In addition there are, on the posterior surface of the postbranchial wall, certain grooves and openings of canals for branches from the subclavian artery. A distinct subclavian ridge (*r. subcl*) is also present separating the marginal vein sinus (*vs. marg*) from the posterior surface of the post-branchial wall.

The marginal vein sinus, which is partly exposed, is large and shaped as usual in *Cephalaspis*-species (*vs. marg*, pl. 10).

The endoskeletal shoulder-girdle (*p. sh*, pls. 9, 10) is exactly as in the Downtonian forms. Of the canals perforating it only the one for the brachial vein (*v. br*, pl. 10) is distinctly seen.

The remaining shield referred with hesitation to the species under consideration is shown in text-figs. 62 and 63. And as is seen from those figures, it is rather imperfectly preserved. In addition it should be added that it is much flattened.

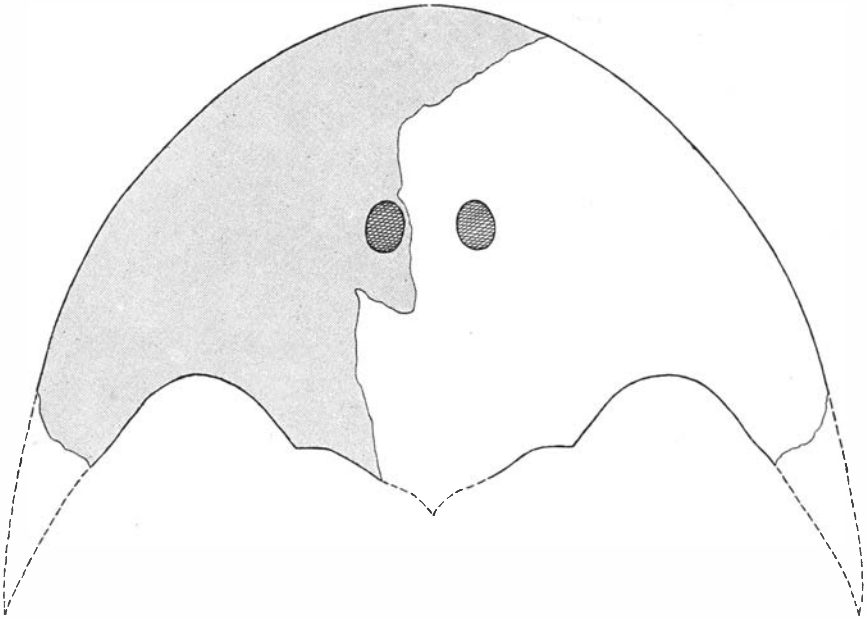
Its length and its breadth were respectively about 9,5 cm. and 17 cm., and it is thus somewhat smaller than the type. As a whole, it is rather suggestive of that, though as is easely seen, it differs from it in certain minor respects. Since these differences, however, may wery well be imagined to have been caused by pressure in the rock it, seems to me

Text-fig. 62. *Cephalaspis höegi* n. sp. Fragmentary cephalic shield. Ventral view. Specimen no. 115. About 5/6 of the nat. size.

at present best not to separate it from the type either as a subspecies or as a species. The ornamentation of the dorsal side consists of numerous small tubercles and the external parts of the exoskeleton are subdivided into numerous small polygonal areas.

Finally the fragment of the cornu which also was doubtfully assigned to *C. höegi* agrees in all respects with the cornu of the last-described shield.

Remarks. — So far as the general shape and ornamentation are concerned the type shield is suggestive of *C. lata*, but it differs, however, distinctly from that especially in the greater length of the cephalic division proper, the distance between the pectoral sinus and the rostral end being about one half of the breadth of the shield measured at the transverse plane trough the anterior end of the pectoral sinuses. In *C. lata* the distance between the rostral end and the pectoral sinus is much less, in fact constituting almost only a third of the breadth at the corresponding transverse plane. Otherwise the type seems to differ from *C. lata* by the more backward direction of the cornua and by its ornamentation. And yet further differences will probably be discovered when new, more complete material is found. In my opinion, however, what is already known, is sufficient to show that we are concerned here with



Text-fig. 63. *Cephalaspis höegi?* n. sp.
Restoration of the outlines of the fragmentary cephalic shield shown in text-fig. 62.
A little more than 2/3 of the nat. zise.

a species which though closely related to *C. lata*, nevertheless is a species of its own. I have named it after Dr. O. HÖEG, Curator of the Botanical Collections of the Academy of Science, Trondhjem, who collected the type specimen during his visit to Spitsbergen in 1924.

The other three specimens are too fragmentarily preserved to be compared with the type with regard to many details. But since, as far as they are known, they are rather suggestive of that they have with hesitation been referred to *C. höegi*.

Geological series horizon and locality. — Wood Bay series, (lower Devonian). Mt. Lyktan on the east coast of Dickson Bay. Specimen no. 11 was collected by O. HÖEG in 1924, the other three specimens by A. HEINTZ in 1925.

10. *Cephalaspis hoeli* n. sp.

(Pls. 17—23; pl. 24, fig. 1; pl. 62, fig. 1; pl. 67, fig. 2; pl. 68; text-fig. 64).

This species seems to be the most common of all the *Cephalaspis*-species in the Spitsbergen Downtonian, being represented by not less than 19 specimens (nos. 18—35 and 39). In addition 7 further specimens (nos. 36—42) may be referred to it with hesitation. All thees 26 specimens consist only of more or less fragmentary remains of the cephalic shield. As a holotype for the species I have chosen specimen no. 22 (pls. 17—18; pl. 19, fig. 1).

The largest cephalic shields attain a length of about 2,5—3 cm. (the dorsal spine not included)[1] and a maximum breadth of about 3—3,4 cm. In the smallest shields known so far the corresponding dimensions are about 1,5 cm. and 1,7 cm. respectively. The height at the posterior end of the dorsal electric field is in the smallest shields about 0,4 cm., in the largest shields about 0,8—0,9 cm. Generally it is difficult to get exact measurements, as most shields are either imperfect in certain respects or considerably flattened or distorted by pressure. As is seen from the figures given, the species was certainly of a small size.

With regard to the general shape of the shield in the species it is obvious that the maximum breadth, which falls rather far anteriorly to the posterior ends of the cornua is only slightly greater than the length from the rostral end to the posterior end of the dorsal spine. In several of the specimens — for instance in the holotype (pls. 17, 18), — there is no distinct rostral angle on the anterior border; in others this angle does occur, though it is rather indistinct. The cornua, which point almost straight backwards, are rather strong and broad and, as is usual in species in which that is the case, they are much flattened in a dorsiventral direction. Their length is approximately one half of that of the shield in the median line (exclusive of the dorsal spine) or slightly more. They lack pectoral angle, and are along their medial margin provided with a series of denticles, which are closely set and have their cusps directed antero-medially. The pectoral sinus is distinct and comparatively deep. The interzonal part corresponds in breadth to about one half of the maximum breadth. It is provided with a rather strong dorsal spine (text-fig. 64; *d. sp*, pl. 19, figs. 2, 3), which appears to be much inclined backwards. The orbital openings are large in proportion to the size of the shield. They are somewhat longer than they are broad, and have their longitudinal axes almost parallel or only very slightly converging forwards. The lateral electric field is rather broad, and extends backwards at least to the middle of the length of the cornu of its side. The dorsal electric field is long and narrow, its maximum width constituting only about one third of its length.

The superficial layer of the exoskeleton was certainly continuous and there are no traces of polygonal areas. The outside of the superficial layer is imperfectly known, but, as far as can be judged, it may in certain specimens (no. 30) be smooth and show only the usual pores, while in others (no. 29) it may be provided with small tubercles at least along the rostral and lateral borders and the ventral rim. Finally in certain cases (no. 29, 31; pl. 67, fig. 2; pl. 68, figs. 2, 3) has been found to have on the ventral rim and the adjacent part of the ventral side of the cornua an ornamentation of chiefly longitudinal ridges, between which the

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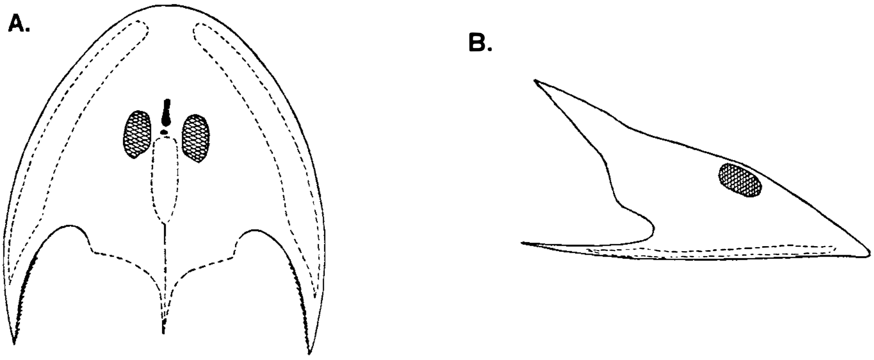
[1] The length measured from the rostral end of the shield to the base of the dorsal spine.



Text-fig. 64. *Cephalaspis hoeli* n. sp.
Restoration of the cephalic shield. *A* in dorsal, *B* in lateral view.

pores lie in longitudinal rows at the bottom of depressions or grooves. In the latter case the structure of the exoskeleton is both in surface view and in transverse section very *Pteraspis*-like (cf. p. 37 above). A similar development of the external layer in the corresponding place is also found in another Downtonian form from Spitsbergen, viz. *C. staxrudi.*

The internal parts of the shield are often found in a very good state of preservation, a fact which has enabled me to study them in detail. The results of my studies are given in full in anatomical part of this monograph (pp. 47—245 above). What there is to be seen of internal structures is well shown in pls. 17—24 and pl. 62, fig. 1.

Remarks. — *C. hoeli* is easily distinguished from other *Cephalaspis*-species by the general shape of the cephalic shield, the shape and direction of the cornua and the shape and direction of the dorsal spine. It has been named in honour of the present leader of the Norwegian explorations of Spitsbergen, Mr. ADOLF HOEL of Oslo University, who has collected the greater part of the material described in this monograph.

The 7 species referred to *C. hoeli* with hesitation are imperfectly preserved and cannot therefore be determined with full certainty; but as far as they are known, they agree most closely with the holotype of *C. hoeli.*

Geological series, horizons and localities. — Red Bay series (Downtonian). In horizons 200 and 250 m. above the sea at the Fränkel Ridge, at the foot of Mt. Pteraspis and in the horizons A, G, J, L, O, and P of Ben Nevis (most specimens). The horizon at Ben Nevis in which the species seems to be most common is J. The majority of the specimens have been collected by ADOLF HOEL in 1909; two — those from the Fränkel Ridge (nos. 26, 42) — have been found by A. HEINTZ in 1925.

11. *Cephalaspis eukeraspidoides* n. sp.

(Pl. 32, fig. 1; text-fig. 65).

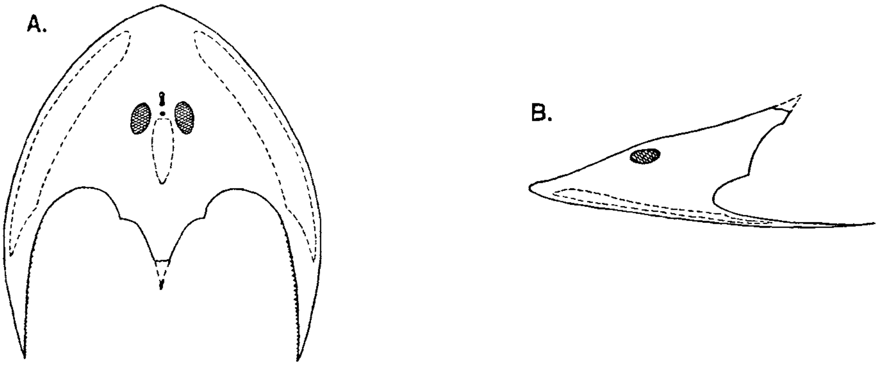
As far can be judged this species is represented only by one cephalic shield (specimen no. 43), which lacks the left cornu and certain other parts.

This shield measures in length from the rostral margin to the posterior end of the dorsal spine 3,7 cm., in breadth between the posterior ends of the cornua about 4,3 cm., and somewhat further anteriorly about 4,7 cm. The breadth thus only slightly exceeds the length. The height just behind the dorsal electric field is about 1 cm. As is obvious from these measurements, the shield is only slightly larger than the largest ones known of *C. hoeli.*

A distinct rostral angle is present. The cornua, which issue backwards, are very long, their length in fact corresponding to somewhat more than two thirds of the length of the shield from the rostral angle to the posterior end of the dorsal spine. In proportion to their length, however, they are comparatively broad and robust. As far as can be seen, they are rather much flattened in a dorsi-ventral direction, and with regard to their general shape it is further worthy of notice, that they are more distinctly arched inwards than those in *C. hoeli.* Along their medial margin they are provided with small denticles, which, at least most anteriorly, seem to be directed almost straight medially with their points. A pectoral angle is absent. The pectoral sinus is distinct and broad. The interzonal part is narrow, attaining a breadt of only 1,4 cm. (measured between the postero-lateral angles) and seems to have been produced into a rather short dorsal spine. On its dorsal side it has a distinct median longitudinal ridge, which from the posterior end of the dorsal electric field extends backwards, probably to the point of the dorsal spine. The orbits, which lie somewhat nearer the rostral angle than the posterior end of the dorsal spine and thus somewhat anteriorly to the middle of the length of the shield, are rather small and have an oval shape with the longitudinal axes slightly converging forwards. The dorsal electric field is rather narrow. The lateral electric field is broad, and appears to have extended backwards on the cornu at least to the middle of the length of that.

The lower side of the cornua is covered by a continuous smooth superficial layer, and, as far as can be judged from that, it seems highly probable that the entire cephalic shield had a similarly developed superficial layer. No traces of polygonal areas can be seen.

Remarks. — The species now described is perhaps at the first glance rather suggestive *C. hoeli*, but on a closer study it appears, however, to differ distinctly from that, especially in the general shape of



Text-fig. 65. *Cephalaspis eukeraspidoides* n. sp.
Restoration of cephalic shield. *A*, in dorsal, *B*, in lateral view.
Aproximately natural size.

the cephalic shield and the greater length of the cornua. On account of its long somewhat Eukerapis-like cornua I have named it *C. eukeraspidoides*.

Geological series, horizon and locality. — Red Bay series (Downtonian). Horizon R, Ben Nevis. Collected by Adolf Hoel in 1909.

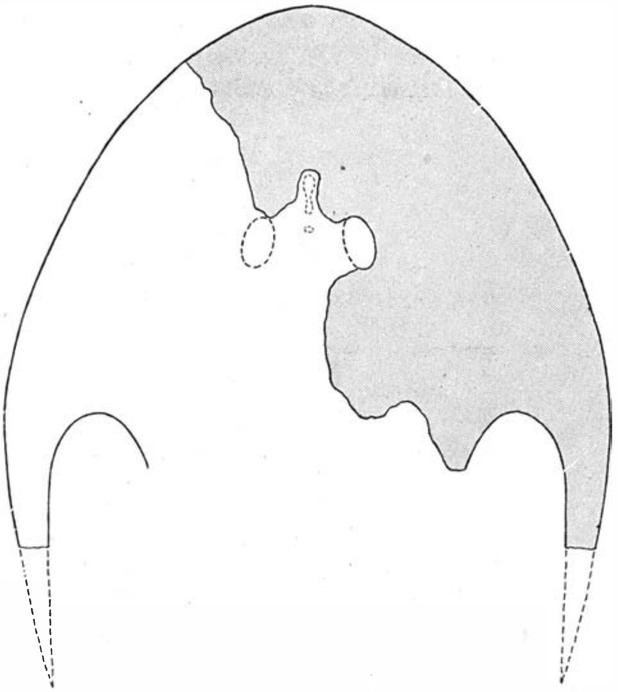
12. *Cephalaspis vogti* n. sp.

(Pls. 25—27; pl. 31, fig. 1; text-fig. 66).

This species is based on an imperfect cephalic shield (specimen no. 46, pl. 27, text-fig. 66). In addition I refer to it, though with hesitation, five still more imperfect cephalic shields (specimens nos. 47—51; pls. 25, 26; pl. 31, fig. 1).

All the shields present are from rather small individuals. In the holotype the dimensions of the shield are as follows: length between the rostral margin and the posterior end present of the interzonal part probably about 3—4 cm., maximum breadth about 4,5—5 cm., and height somewhat behind the orbits about 1,5 cm. No more exact measurements than these are to be had.

As is seen, the breadth of the cephalic shield of the holotype thus only slightly exceeds the length. A rather distinct rostral angle is found both in the holotype and in shield no. 46. The cornua, which issue in a backward and probably somewhat medial direction, are only known in their proximal parts, but from what is preserved of them it is, however, fully clear that they are rather slender and flattened in a dorsi-ventral direction. Their medial margin is provided with a few rather narrow antero-medially curved denticles. No pectoral angle is present. The pectoral sinus is well developed, but rather narrow in transversal direction, while the interzonal part is strikingly broad. The



Text-fig. 66. *Cephalaspis vogti* n. sp.
Restoration of cephalic shield based on specimen no. 46. $^7/_4$.

detailed shape of that part is not known as its posterior portions are missing. At least in the holotype the orbital openings, which probably are situated somewhat nearer to the rostral than to the posterior end of the shield, are in shape and have their longitudinal axes slightly converging forwards. The shape and extent of the dorsal electric field are unknown. The lateral electric field ends backwards already on the proximal part of the cornu of its side.

The superficial layer of the exoskeleton is continuous and smooth. As usual it is perforated by numerous closely set pores. The appearence of it is well shown in pl. 31, fig. 1, (*sl;* from specimen no. 47). There are probably no traces of polygonal areas.

As is seen from pls. 25—27, numerous canals for vessels and nerves and parts of the cranial cavity and of the ears etc. are well preserved in certain of the specimens referred to this species.

Remarks. — *C. vogti* differs from other species known especially by the general shape of the cephalic shield and by the rather slender postero-medially directed cornua. It has been named in honour of Dr. Th. Vogt, State Geologist, of Oslo, who was the leader of a Norwegian expedition in 1925 for the exploration of the Downtonian and Devonian deposits of Spitsbergen.

Specimens nos. 47—51 are too imperfectly preserved to be determined with full certainty, but, as far as they are known, they agree, however, most closely with *C. vogti*, and I have therefore provisionally referred them to that species.

Geological series, horizons and localities. — Red Bay series (Downtonian). All the specimens — except no. 51 which is from the Fränkel Ridge, 200 m. above the sea — were found in the lower horizons of Mt. Pteraspis. Five of the specimens (nos. 46—50) were collected by ADOLF HOEL in 1912; the remaining one (no. 51) was collected by A. HEINTZ in 1925.

13. *Cephalaspis heintzii* n. sp.

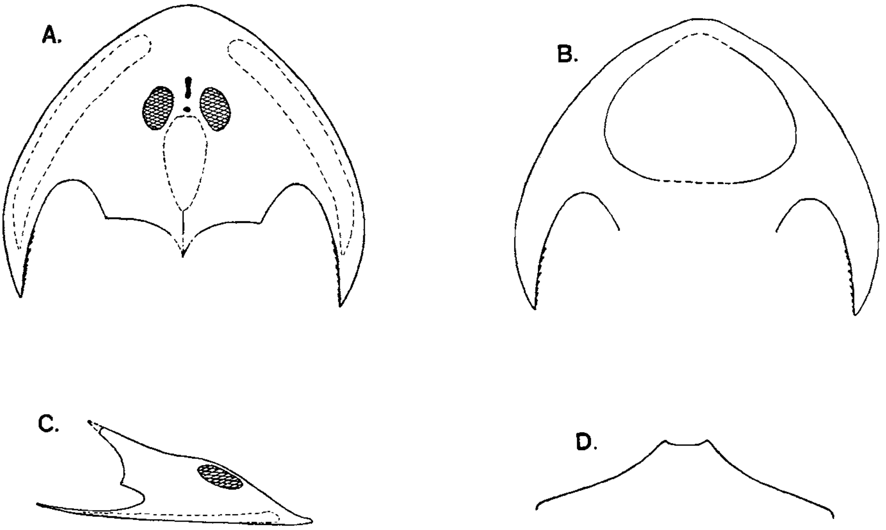
(Pls. 29, 30; pl. 31, fig. 3; pl. 35, figs. 1, 2; pl. 36, figs. 1—3; text-fig. 67).

Under this species name are gouped three imperfect cephalic shields (specimens nos. 52, 53, 54). As a holotype I have chosen the most complete one of the three (specimen no. 52). In addition a fourth imperfect shield (specimen no. 68) may perhaps pertain to this species.

The dimensions of the shields are as follows:

	No. 52.	No. 53.	No. 54.	No. 68.
Length from rostral to posterior angle	2,1 cm.	3,3 cm.	about 4 cm.	about 6 cm.
Maximum breadth (somewhat in front of the posterior ends of the cornua)	3,3 „	about 5,5 „	„ 6 „	„ 10 „
Distance between the posterior ends of the cornua	2,95 „	—	—	—
Height at the posterior end of the dorsal electric field	0,8 „	„ 1 „	„ 1 „	—
Breadth of the interzonal part of the shield	1,5 „	„ 2,7 „	—	„ 4,6 „

The four shields have all been partly affected by pressure, and certain of their dimensions may therefore originally have been somewhat different from what they are in the present state of preservation. It is quite obvious, however, that the bredth was considerably greater than the length. The rostral angle is developed, though obtuse. The cornua are rather broad and strong and flatened in dorsi-ventral direction. In the holotype they are directed almost straight backwards and appear to be slightly curved inwards; in the three other specimens (nos. 53



Text-fig. 67. *Cephalaspis heintzi* n. sp. Restoration of cephalic shield based on specimen no. 52. *A*, in dorsal view, *B*, in ventral view, *C*, in lateral view, *D*, in transversal section somewhat behind the orbits. 3/2.

54, and 68), on the contrary, they seem to have pointed somewhat more laterally and to be straighter. The holotype has the medial margins of the cornua provided with small denticles, which are curved in such a way that they point antero-medially, whereas in the shields no. 54 and no. 68, which both have a proximal part of the left cornu preserved, there are no traces of denticles. As the shield no. 54 is in a rather bad state of preservation and appears to have been abraded, and as the shield no. 68 also is very imperfect, it seems very probable that these two shields originally had denticles too on their cornua but lost them before the embedding in the rock. The pectoral sinus is well developed, but rather narrow. The interzonal part is rather short and, at least in the shields nos. 52 and 53, it is in addition broad. In the shield no. 54 only a very small part of it is left, but, as far as can be judged, it seems to have been somewhat narrower than in the former two shields. The orbital openings, which are large and oval, with the longitudinal axes more or less converging forwards, lie anteriorly to the middle of the length of the shield. The dorsal electric field is rather broad, with the broadest place in the anterior half. From its posterior end a low median ridge passes backwards to the posterior end of the posterior angle. The lateral electric field is well developed and reaches far backwards on the cornu.

The holotype exhibits a portion of the oralo-branchial fenestra (text-fig. 67 B; *obr. f.*, pl. 36, fig. 3), which appears to be broader than it is long. And the shield no. 68 shows very beautifully many of the canals for vessels and nerves (pls. 29, 30; pl. 31, fig. 3).

On account of the bad state of preservation of the external layers of the exoskeleton of the shields the ornamentation is entirely unknown. The external parts of the exoskeleton are not subdivided into polygonal areas.

Remarks. — The shield no. 52 described here obviously cannot be referred to any known species, but must represent a new one. For that new species I have proposed the name *heintzi* after ANATOL HEINTZ, Conservator at the Paleontological Museum, Oslo, who was a member of Dr. TH. VOGT's Spitsbergen expedition in 1925 and who collected several of the Cephalaspids described in this monograph.

The shields no. 53 and 54 resemble the type (no. 52), and I have therefore felt it necessary to refer them to the same species as that. Specimen no. 68 is too imperfect to be determined with full certainty but as all its characters preserved are mostly as in the species here under consideration I have found it most convenient at present to place it here provisionally.

Geological series, horizons and localities. — Red Bay series (Downtonian). Shield no. 52 is from the Fränkel Ridge, 200 m. above the sea; shield no. 53 is from Ben Nevis but there are no exact data concerning the horizon; and shields no. 54 and no. 68 were found in horizons *O* and *J* respectively at Ben Nevis. Specimens nos. 54 and 68 have been collected by A. HOEL in 1909 and specimens 52 and 53 by A. HEINTZ in 1925.

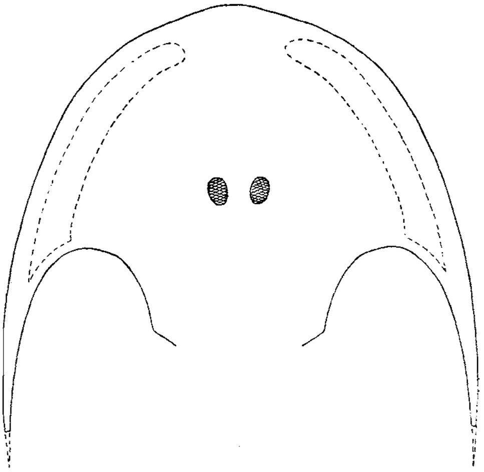
14. *Cephalaspis staxrudi* n. sp.

(Pl. 34; pl. 36, fig. 4; pl. 37, figs. 1, 2, text-fig. 68, 69).

This species is based on a fragmentarily preserved cephalic shield (no. 56, pl. 37, fig. 1), text-fig. 68. In addition I refer to it though with hesitation a second larger specimen (no. 57, pl. 34; pl. 36, fig. 4, text-fig. 69), which is represented by a considerable part of the cephalic shield and certain of the scales of the anterior part of the trunk.

The holotype (no. 56) is about 4,5 cm. (long from the rostral end to the posterior end of the interzonal part) and about 6 cm. broad at the broadest place, which is situated rather far back between the middle parts of the cornua, whereas its height is only 0,8 cm. at the highest place in the interzonal part. The other cephalic shield (no. 57) is much larger, its dimensions being: length about 17 cm., maximal breadth about 24 cm., and maximal height about 3 cm.

For a detailed description we first turn to the holotype (text-fig. 68; pl. 37, fig. 1). As is obvious from the measurements given, this is somewhat broader than it is long and strikingly flat. A rostral angle is present, though rather indistinct. The cornua, which issue almost straight backwards, are long and slender, their length constituting about $^3/_4$ of the



Text-fig. 68. *Cephalaspis staxrudi* n. sp. Restoration of cephalic shield after specimen no. 56. 1/1.

length of the shield from the rostral angle to the hindmost preserved portions of the interzonal part. They probably lack denticles on the medial margin. The pectoral sinus is deep and broad and wery well developed, and as a consequence of this the interzonal part is rather long and comparatively narrow. Concerning the interzonal part it should further be mentioned that the posterior portions of it are missing and that because of this condition the exact configuration of its posterior margin cannot be ascertained. The orbital openings — which are small, with their longitudinal axes diverging forwards — are situated strikingly far back, in fact probably slightly behind the middle of the length of the cephalic shield measured from the rostral angle to the posterior preserved portion of the interzonal part. Moreover it is also clearly seen that they lie strikingly far back in relation to the pectoral sinus. The dorsal electric field is very imperfectly preserved, so that nothing can be ascertained concerning its shape. The lateral electric field is broad even posteriorly and extends only a short distance backwards on the cornu of its side.

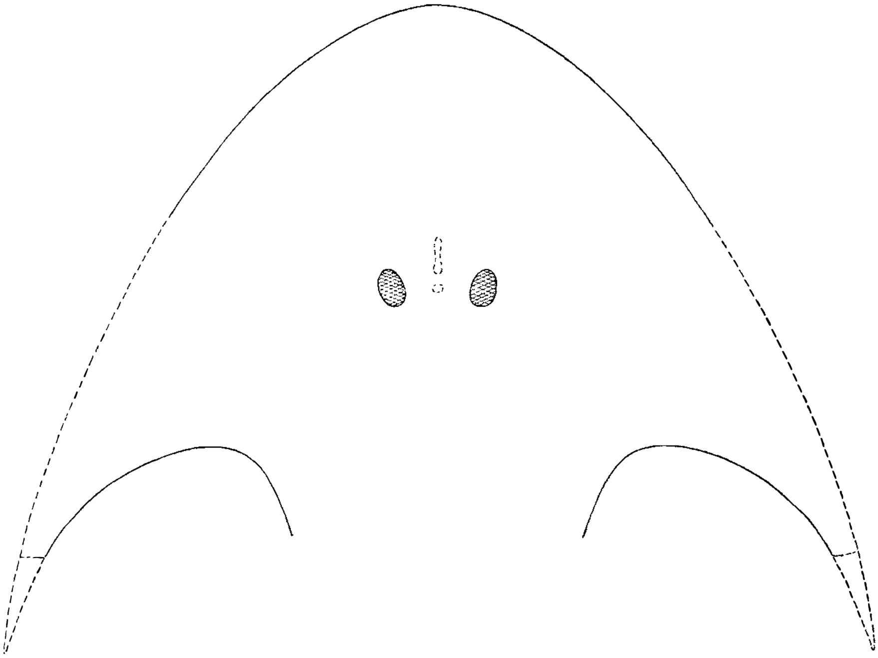
The exoskeleton consists of the ordinary three layers. And the superficial layer was certainly continuous. On the lower side of the shield it is clearly seen (pl. 37, fig. 2) that that layer is provided with ridges concentric with the lateral borders of the shield, and that the pores that regularly traverse it are situated in rows in shallow grooves between the ridges. As a whole, therefore, the external parts of the exoskeleton at this place are in fact suggestive of the external parts of the exoskeleton of the Pteraspids. In this connection it deserves to be pointed out that the lower side of the shield may be developed in a similar way also in *Cephalaspis hoeli* (pl. 67, fig. 2; pl. 68; cf. also p. 37 above).

The other shield (no. 57) referred with hesitation to the species (text-fig. 69; pl. 34, figs. 1—4) resembles the type rather much with regard to its general shape, but is more pointed anteriorly than that. Unfortunately its cornua are imperfectly preserved, so that it is not possible to say with certainty whether these were of the same shape as in the type or whether they were shorter. Likewise it is not possible to decide with certainty whether they issued in a similar direction as in the type or whether they were as in the restoration given in text-fig. 69. The pectoral sinus and the interzonal part agree in essentials with those in the type. The dorsal electric field was certainly rather broad, at least in the anterior parts, but is very imperfectly preserved (pl. 34, fig. 1). Ventrally to the oralo-branchial chamber, or in the ventral part of that, there are found a few of the small more or less irregular oblonge scales, which were present on the external side of the soft tissue that closed the oralo-branchial fenestra.

The exoskeletal bone is preserved only on the lower side of the shield, thus only on the ventral rim and on the ventral sides of the cornua. It was rather thick, with the middle layer well developed. The superficial layer seems not to have been continuous, but represented only by numerous tubercles, between which the middle layer was discernible. These tubercles are all rather small in proportion to the size of the shield, but it is clearly seen that they are relatively larger on the anterior parts of the ventral rim than on the lower side of the cornua, where most posteriorly they even become very small. In addition it is worthy of notice in this connection that the tubercles are blunt and irregularly lobated, on the anterior part of the ventral rim (pl. 34, fig. 2), while more backwards towards the cornua they are blunt and somewhat elongated and arranged with their longitudinal axis concentrically with the lateral border of the shield (pl. 34, figs. 3, 4); most posteriorly on the ventral side of the cornua they are badly preserved, but, as far as can be judged, they are rounded and somewhat pointed. As is thus seen, the ornamentation is very different from that in the type. Since, however, in such a form as *Hemicyclaspis (Cephalaspis) murchisoni* and *C. hoeli* I have found that the ornamentation is subject to considerable variations, it is very likely that this is the case also in other species and that it therefore perhaps is of much less importance as a species character than has been supposed hitherto.

Finally, as has already been mentioned, there are associated with the shield just described (no. 57) certain of the anterior flank scales of the trunk (pl. 36, fig. 4). More exactly, these scales belong to the deep middle series and to the ventro-lateral fringe series. They are all composed of three layers, like the exoskeleton of the shield. The superficial one of these layers was perhaps continuous and had at least in places tuberculations on its outer surface. In other places it seems as if the ornamentation on its outside had consisted of fine parallel striaae with a chiefly dorsi-ventral arrangement.

Remarks. — The holotype reminds one in its general shape somewhat of *C. Salweyi*, but it is nevertheless obvious that it represents a new species, which is characterized by the general shape of the cephalic shield, by the long slender rapidly tapering cornua, the large pectoral

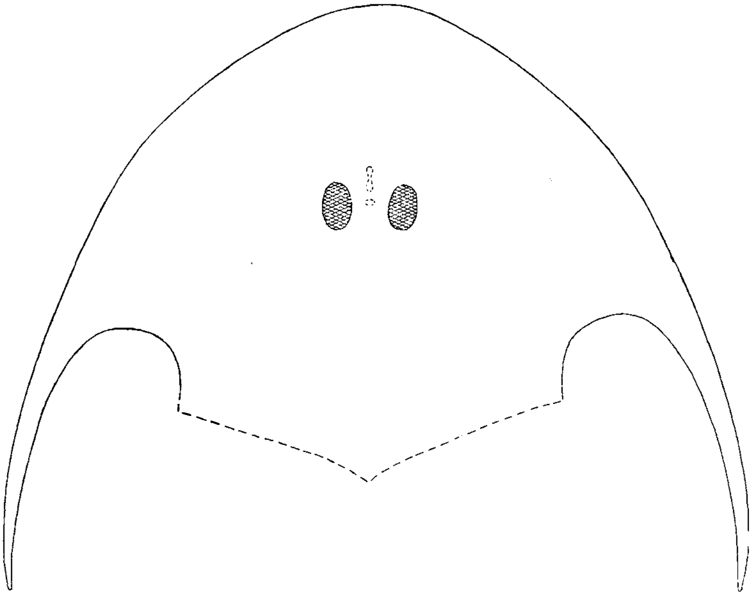


Text-fig. 69. *Cephalaspis staxrudi*? n. sp. Restoration of cephalic shield (after specimen no. 57). The exact shape, length and direction of the cornua uncertain. Somewhat less than one half of the nat. size.

sinus, the rather narrow interzonal part and the position of the small orbits rather far backwards. This new species has been named after captain A. STAXRUD, who was a member (1906, 1909, 1919, 1920) and one of the leaders (1911—1914) of certain of the Spitsbergen expeditions during which parts of the material dealt with in this monograph were collected.

The other shield described (no. 57) is beyond question rather suggestive of the type, but it differs, however, somewhat from that both in its general shape and in its ornamentation. The differences in the general shape cannot be considered to mean very much, since they may very well be imagined to be due to the rather considerable distortion of the specimen. The difference with regard to ornamentation seems also to be of slight importance, since it is now known that in different specimens of certain other species it may exhibit considerable variations. Under these circumstances I have considered it best not to establish any new species for the shield in question, but to refer it provisionally to *C. staxrudi.*

Geological series, horizons and locality. — Both the shields described here are from the Red Bay series (Downtonian) and both have been found at Ben Nevis, the type (no. 56) in horizon *H*, the other one (no. 57) in a horizon 600 m. above the sea near horizon *N*. The holotype was collected by A. HOEL in 1909, the other specimen (no. 57) by A. HEINTZ in 1925.



Text-fig. 70. *Cephalaspis spitsbergensis* n. sp. Restoration made after the type specimen (no. 58). 3/5.

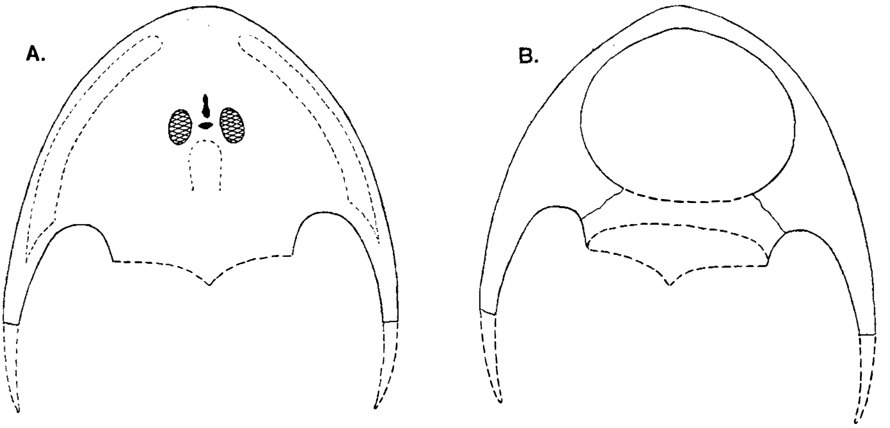
15. *Cephalaspis spitsbergensis* n. sp.

(Pl. 33, fig. 1; pl. 35, fig. 3; pl. 39; pl. 40; fig. 2; text-figs. 70, 71).

This species is established for a fragmentary cephalic shield (specimen no. 58; pl. 33, fig. 1). In addition I refer provisionally to it a second also fragmentary cephalic shield (specimen no. 59, pl. 35, fig. 3, pl. 39; pl. 40, fig. 2).

The first-mentioned one of these two shields must have attained a length of about 8,5—9 cm. (measured from the rostral angle to the posterior end of the interzonal part), a maximum breadth (at or close to the posterior ends of the cornua) of about 13—14 cm., and a maximum height of about 3 cm. The other shield (specimen no. 59) is considerably smaller, its corresponding dimensions being about 5 cm., 7,3 cm. and 1,9 cm. respectively.

In both shields there is only a slight indication of a rostral angle. The cornua, which issue backwards and somewhat laterally, are long and slender, with the distal parts almost circular in transverse section. It should also be noticed here that in the type (text-fig. 70) they appear to be only very slightly curved inwards, whereas in the other specimen they are fairly strongly curved in that direction. At least in their present state of preservation they exhibit no certain traces of denticles. The pectoral sinus is well developed and deep. And the interzonal part, which is imperfectly preserved posteriorly, is broad, constituting not less than about one half of the maximum breadth. The orbital



Text-fig. 71. *Cephalaspis spitsbergensis* n. sp. Restoration made after specimen no. 59. A, in dorsal, B, in ventral view. 2/3.

openings of shield no. 58 are rather small and seem to have occupied such a position that their longitudinal axes diverged forwards, whereas those of shield no. 59 seem to be a little larger and are situated so that their longitudinal axes converge forwards. In the type there are no distinct remains of the electric fields. In shield no. 59 both the dorsal and the lateral of these fields are to be seen, though in an imperfect state of preservation. But as far as can be judged, their shape and extension were approximately as shown by text-fig. 71.

In both specimens the ornamentation consists of numerous fairly small tubercles. On the ventral rim (pl. 35, fig. 3) these tubercles are rather irregular in shape and are also irregularly set; further backwards, on the lower side of the cornua, they may be slightly elongated in the longitudinal direction of the cornua and may also exhibit a more or less distinct tendency to be arranged in longitudinal rows. Whether the exoskeleton was subdivided externally into polygonal areas cannot be decided with certainty. But at least in shield no. 59 it is not very likely that this was the case.

In shield no. 58 a dorsal part of the postbranchial wall and certain traces of the bone-layer lining the oralo-branchial chamber are to be seen.

Remarks. — Though very imperfectly known, the shield no. 58 shows, however, beyond question that it cannot be referred to any of the other species described of the genus. Its most striking characters are the general shape and proportions of the cephalic shield and the long slender cornua.

As far as it is known, shield no. 59 differs from the type only in certain characters, which appear to be of rather small importance. And because of this I have found it most convenient to refer it, at least provisionally, to this species.

Geological series, horizons and localities. — Red Bay series (Downtonian). Shield no. 58 is from horizon *R* of Ben Nevis; shield no. 59 from an horizon 200 m. above the sea at the Fränkel Ridge. The type shield (no. 58) was collected by ADOLF HOEL in 1909, the other shield (no. 59) by A. HEINTZ in 1925.

16. *Cephalaspis kolleri* n. sp.

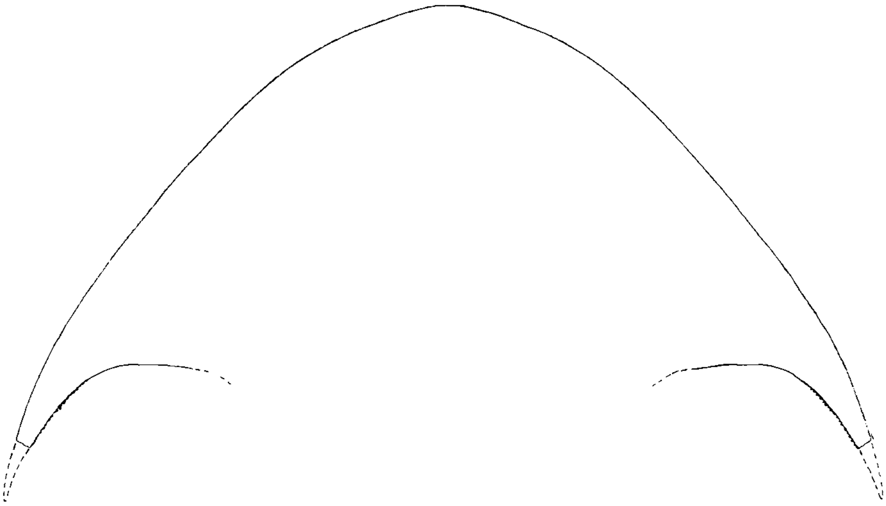
(Pl. 31, fig. 2; pl. 32, fig. 3; pl. 43, fig. 2; text-fig. 72).

The holotype for this species is a ventral portion of the cephalic shield (specimen no. 60, pl. 32, fig. 3) with parts of the right cornu. Besides the holotype two other shields seem to pertain to the species. One of these two shields (no. 64, pl. 31, fig. 2) is represented by the right cornu and an adjacent part of the ventral rim of the right side, the other (no. 61, pl. 43, fig. 2), on the contrary, by hardly more than the left cornu. Finally I refer to this species with hesitation two detached cornua (specimens no. 62, and no. 63).

The type shield was at least 12 or 13 cm. long from the rostral angle to the posterior end of the interzonal part, and probably about 27 cm. broad between the posterior ends of the cornua. It was thus from a very large individual. The parts present of shield no. 61 are from an animal of similar size as the type, while the parts preserved of shield no. 64 are from a considerably smaller one. Both the fragments which have been placed with hestitation to the species are from large individuals.

As far as can be judged. the type shield must have had a shape approximately as shown by text-fig. 72. It was thus about twice as broad as it was long. It has only a very slight indication of a rostral angle. The cornua, which are rather small in proportion to the size of the shield, are directed rather much laterally, about as much as in *C. brevicornis*. In their approximal parts they are broad, but taper rapidly distally; and as a whole they are therefore more slender than in the species just mentioned. In addition they are also curved somewhat differently from what they are in that. They are much flattened in a dorsi-ventral direction and their medial margin is provided with small denticles, which seem to have been rather straight or at least only very slightly curved forwards. The pectoral sinus was probably broad and rather shallow. The interzonal part is very fragmentarily preserved so that its shape is unknown. The orbital openings and the dorsal electric field are not preserved. Parts of the lateral electric field are present, but they are not well accessible for investigation, so that the shape and extension of that field still remain unknown.

The exoskeleton was evidently rather thick and strong. It is ornamented throughout by numerous, rather small, closely set tubercles, which on the ventral side of the cornua and the adjacent parts of the ventral rim may be somewhat elongated, with the longest axes more or



Text-fig. 72. *Cephalaspis kolleri* n. sp. Probable outlines of cephalic shield. After specimen no. 60. 1/2.

less distinctly concentric with the lateral margins of the shield. Whether the superficial layer was present only in the tubercles or whether it also occurred between these could not be made out. The external parts of the exoskeleton are, at least on the dorsal side of the shield, subdivided into polygonal areas.

Remarks. — *C. kolleri*, which I have named after engineer A. KOLLER of Oslo, who has taken part in several of the Norwegian Spitsbergen expeditions (1906, 1909—1914, 1917—1925), greatly resembles *C. brevicornis* from the Spitsbergen Devonian with regard to the general shape of the cephalic shield. It is, however, easily distinguished from that by the less pronounced rostral angle by the larger breadth in the rostral parts, by its more slender and differently curved cornua, and by its ornamentation.

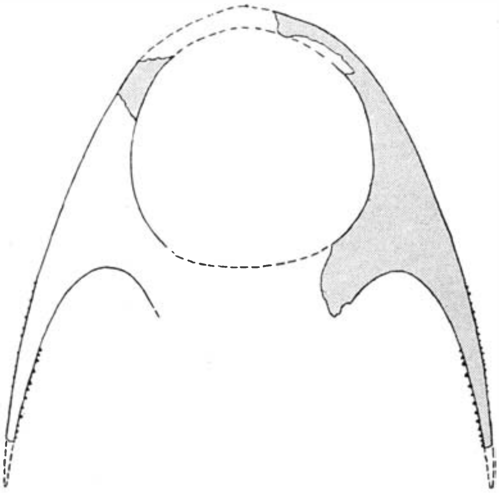
The specimens which I have referred to *C. kolleri* with hesitation are too imperfect to be determined with certainty; but as far as they are known, they seem to agree well with *C. kolleri.*

Geological series, horizons and localities. — Red Bay series (Downtonian). Horizons P (specimen no. 60), L (specimen no. 62) and the Cliff (specimen no. 61), Ben Nevis; Mt Pteraspis (specimen no. 63). The specimens have probably all been collected by A. HOEL in 1909 (Ben Nevis) and 1912 (Mt Pteraspis).

17. *Cephalaspis gracilis* n. sp.

(Pl. 38, figs. 2, 3; text-fig. 73).

This species is based on a specimen (no. 65) which is represented by the left cornu and a considerable part of the ventral rim. As far as can be judged from these remains, the outlines of the cephalic shield were approximately as shown in text-fig. 73.



Text-fig. 73. *Cephalaspis gracilis* n. sp. Probable outlines of cephalic shield. After specimen no. 65. 3/4.

The cephalic shield seems to have had a length of about 6 cm. (measured from the rostral end to the supposed posterior end of the interzonal part), whereas its maximum breadth probably amounted to about 7 cm. Thus the maximum breadth seems to have been only slightly larger than the lenght.

The rostral margin is imperfect (text-fig. 73; pl. 38, fig. 3), and it is therefore impossible to say wheter there was any rostral angle or not. The coruna, which project backwards and slightly laterally, are long and slender, constituting about three quarters of the length of the shield. They are flattened in a dorsi-ventral direction throughout their length, and their medial margins are provided with straight denticles, which are fairly sparse, so that there are rather considerable intervals between them. Similar though smaller denticles were probably also present on their lateral margins. The pectoral sinus is comparatively broad and well developed. The interzonal part, on the contrary, seems to have been rather narrow, but is so imperfect that its detailed shape cannot be ascertained. The oralo-branchial fenestra seems to have been almost circular or only slightly longer than broad (text-fig. 73).

The ornamentation is unknown. The exoskeleton in the parts present of the shield have no distinct traces of polygonal areas.

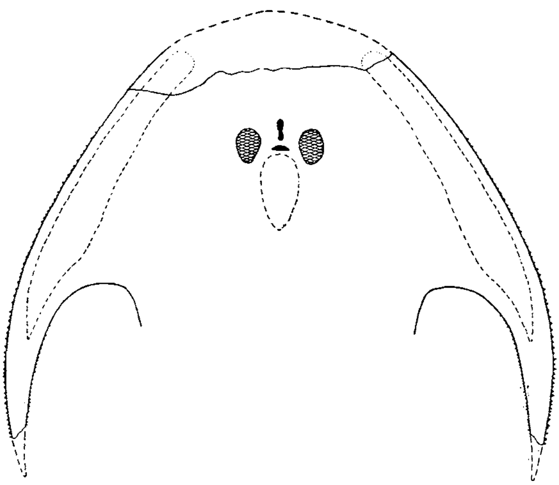
Remarks. — As far as can be judged, specimen no. 65 represents a new species, which is characterized by the comparatively narrowness of the cephalic shield and the long slender dorsi-ventrally flattened cornua.

Geological series, horizon and locality. — Red Bay series (Downtonian). On a loose slab found at Ben Nevis. Collected by Adolf Hoel in 1909.

18. *Cephalaspis arcticus* n. sp.

(Pl. 24, fig. 2; pl. 28; pl. 37, fig. 4; pl. 38, fig. 1; pl. 40, fig. 5; text-fig. 74).

This species is established for a cephalic shield (specimen no. 66, pl. 38, fig. 1) on which certain anterior portions of the interzonal part and a considerable piece of the right cornu are missing. In addition I refer to this species, with hesitation, two other cephalic shields (specimen no. 67; pl. 28; pl. 37, fig. 4; and specimen no. 69; pl. 40, fig. 5), which also are rather imperfectly preserved.



Text-fig. 74. *Cephalaspis arcticus* n. sp. Restoration of cephalic shield. After specimen no. 66. 1/1.

In the shield chosen as a holotype the length from the rostral end to the posterior end of the interzonal part may be estimated at about 4,5 cm., whereas the maximum breadth is about 6,5 cm. The corresponding dimensions in another shield (specimen no. 67) may be estimated at about 5 cm. and 8 cm., respectively. Finally the third shield (specimen no. 69) is so imperfect that no measurements of it can be given, but it is clear that it is from a rather small individual.

We first deal with the type shield (no. 66; pl. 38, fig. 1). This is imperfect anteriorly, but, so far as can be judged, it must have been approximately as shown in text-fig. 74. Wheter a rostral angle was present cannot be decided. The cornua, which are well developed but rather slender and slightly curved inwards, issue in a posterior and somewhat lateral direction as in most forms. They are further characterized by the fact that they are provided with small straight denticles, not only on the medial but also on the lateral margin, and that the denticles on the former margin are somewhat shorter than those on the latter. The pectoral sinus is rather deep and distinct. The interzonal part is broad, but otherwise nothing is known concerning its shape. The orbital openings, which are rather small with the longitudinal axes almost parallel, are situated anteriorly to the middle of the length of the shield and in fact strikingly far forwards. The dorsal electric field is short and broad, its maximum breadth, which is situated in the anterior half, constituting more than one half of the total length. From the posterior end of this electric field a median ridge goes backwards on the interzonal part. The lateral electric field is well developed and as a whole narrower in the anterior half than in the posterior one. It reaches backwards on the cornu of its side, though not as far as the middle of that. The superficial layer of the exoskeleton could not be studied in detail and it is therefore not possible to say whether it was continuous or not. It is clear, however, that it had numerous small rather blunt rounded tubercles both on the dorsal and on the ventral side of the shield. The external parts of the exoskeleton show only very faint traces of polygonal areas.

The best preserved one (no. 67) of the two shields hesitatingly placed under this species (pl. 24, fig. 2; pl. 28) was conceivably of a similar shape as the type and, exactly like that, it has the orbital openings situated strikingly far forwards. On the other hand it is impossible to say whether its cornua were directed exactly as in the type and whether they had any denticles. With regard to its ornamentation the shield in question differs somewhat from the type, inasmuch as, at least on the ventral rim and the ventral side of the cornua, its tubercles are somewhat elongated with the longitudinal axes concentrically with the lateral margin (pl. 24, fig. 2; pl. 37, fig. 4). The shield under consideration shows beautifully several internal details of much interest (pl. 28).

Finally the second shield (no. 69) hesitatingly placed to the species (pl. 40, fig. 5) is represented merely by an antero-dorso-medial part, with the orbits, the dorsal electric field and a number of canals. It shows clearly that the rostral margin is very obtuse, that the orbits lie strikingly far forward and that the dorsal electric field is of a rather similar shape as in the type. The superficial layer is continuous and probably smooth. Accordingly this shield differs from the other two particularly with regard to ornamentation.

Remarks. — Shield no. 66 differs distinctly from that of all other known Cephalaspids with regard to the general shape and in the position of the orbits far forward, and it therefore certainly represents a new species.

Shield no. 67 agrees well, as far as it is preserved, with shield no. 66 with regard to the general shape, but seems to differ to a certain extent from that as regards the ornamentation, and it is therefore not fully certain whether it really pertains to *C. arcticus*. Shield no. 69, also has several of its general characters known so far in accordance with *C. arcticus*, but differs still more from that especially in its ornamentation and may therefore perhaps belong to a species of its own.

Geological series, horizons and localities. — Red Bay series (Downtonian). The type (no. 66) is from a horizon 250 m. above the sea of the Fränkel Ridge; shield no. 67 has been collected in horizon *E* or *F* of Ben Nevis and shield no. 69 in horizon *T* of the same mountain. The shields no. 67 and 69 have been collected by ADOLF HOEL in 1909, the shield no. 66 by A. HEINTZ in 1925.

19. *Cephalaspis apicalis* n. sp.

(Pl. 37, fig. 3; pl. 40, fig. 4).

Under this species name I describe two fragmentary and badly preserved cephalic shields (specimens no. 75, and no. 76). As a holotype I chose the one figured in pl. 37, fig. 3 (no. 75).

Both shields are from rather small individuals, but on account of their imperfect state of preservation no definite measurements can be given.

Concerning the general shape of these shields very little is known. It seems, however, as if their breadth had been rather small. The rostral portion appears to be produced into a very pronounced rostral angle or, in the type, even into an obtuse rostral process. The type has an anterior part of the lateral electric field preserved, whereas the other shield displays the orbits and an anterior part of the aortal ridge.

The ornamentation is entirely unknown. The external parts of the exoskeleton show no traces of polygonal areas.

Remarks. — The type (specimen no. 75), though it is very imperfect, nevertheless has in its somewhat produced rostral end a character by which it differs from all other species known. It is true that in this respect it is somewhat suggestive of the Canadian species *G. campbelltonensis*, but it is, however, fully obvious that it cannot be identical whit that.

The other shield (no. 76), as it has its rostral end less distinctly produced, may perhaps, when new and more complete material of it is found, reveal itself as a different species. Provisionally, however, I have referred it to this species.

Geological series, horizons and locality. — Red Bay series (Downtonian), horizons *G* (no. 75) and *J* (no. 76) of Ben Nevis. Collected by ADOLF HOEL in 1909.

20. *Cephalaspis* n. sp.?

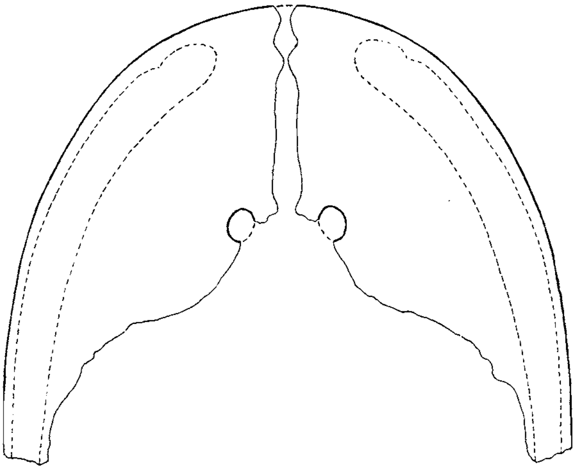
(Pl. 62, fig. 2; text-fig. 75).

The material which I describe here consists of a fragment of a large cephalic shield (specimen no. 77; pl. 62, fig. 2).

The length and the maximum breadth of the shield may be estimated at at least 10 cm. and 14 cm. respectively, but no exact figures of these measurements can be given. The height just behind the orbits was probably about 3 cm. and seems thus to be rather considerable. Accordingly the shield is from a rather large animal.

The shape of the shield cannot be ascertained with certainty, but it seems to me very likely that it may have been somewhat as is shown in text-fig. 75. The orbital openings are strikingly small. The lateral electric field is well developed and rather broad and it certainly reached far backwards on the cornua of its side.

The superficial layer of the exoskeleton is continuous and smooth, at least along the lateral margin of the ventral rim. Othervise nothing is known of the ornamentation. The external parts of the exoskeleton were subdivided into numerous polygonal areas.



Text-fig. 75. *Cephalaspis* n. sp. ?
Possible outlines of the antero-lateral parts of
the cephalic shield. 1/2.

Remarks. — The shield now described resembles in certain respects that of *C. spitsbergensis*, but seems to have the orbital openings smaller than in that species; and, if my opinion concerning the outlines of the shild is true, it further differs from that in the general configuration. Accordingly it is not improbable that it may represent a new species.

Geological series horizon and locality. — Red Bay series (Downtonian); horizon *M*, Ben Nevis. Collected by ADOLF HOEL in 1909.

Cephalaspis remains indeterminable as to species.

In the collection of Spitsbergen Cephalaspids available to me there are, both from the Wood Bay series and from the Red Bay series, a great number of remains which undoubtedly pertain to the genus *Cephalaspis*, buth which are too imperfectly preserved to be determined as to species. Most of these remains are too inconsiderable or otherwise too poorly preserved to be of any interest. A few, however, are more complete or exibit certain details which may be of value from a classificatory point of view and these will be treated here. They have the following numbers 14, 15, 16, 17, 86, 106, P. 550, 109, 83, 78, 79, 80, 87, 88 and 113.

Specimen no. 14 (pl. 11) consists of a part of the right half of a big cephalic shield, with the right cornu preserved in the entire length. The cornu which is long and strong, seems to be devoid of denticles but has an obtuse pectoral angle. The pectoral sinus (*ps*) is rather distinct. The right lateral electric field (*lsf*), except for a short anterior part, is shown in its entire length and appears to be rather narrow and to have extended far back on the cornu. Owing to the much weathered condition of the specimen nothing certain can be ascertained concerning the ornamentation.

Geological series, horizon and locality. — Wood Bay series (lower Devonian), Wood Bay.

Specimen no. 15 (pl. 2, fig. 3) consists like the previous specimen, of a right cornu with adjacents parts of the cephalic shield. It is from a smaller individual than that specimen, but seems otherwise to resemble that rather much. Its ornamentation is unknown.

Geological series, horizon and locality. — Wood Bay series (lower Devonian), S. E. of the ridge between the Arla and Serla glaciers. Collected by A. HOEL in 1910.

Specimen no. 16 (pl. 2, fig. 1) consists of a portion of a left cornu and is from a rather large animal. On the lower side (the one shown in pl. 2, fig. 1) it exhibits in one place (denoted by an white arrow in the plate) traces of a rather fine tuberculation. A similar tuberculation is shown also by specimen no. 110 (pl. 61, fig. 3).

Geological series, horizon and locality. — Wood Bay series (lower Devonian). West side of Wood Bay. Collected by G. WATNELIE in 1910.

Specimen no. 17 (pl. 6, fig. 2) is chiefly an impression of an anterior part of a large cephalic shield. It shows a very obtuse rostral margin without indications of a rostral angle, further the orbital openings, which seem to have been very small in proportion to the size of the shield, and finally the nasal and pineal openings. The ornamentation is not known.

Geological series, horizon and locality. — Wood Bay series (lower Devonian), Wood Bay. Collected 1909, 1910 or 1912.

Specimen no. 86 (pl. 16, fig. 1) is an imperfect impression of a postero-lateral part of a big cephalic shield. It has a broad rather indistinctly defined pectoral sinus, but exhibits otherwise little of interest. The superficial layer of the exoskeleton is smooth and continuous. And there are no traces of polygonal areas.

Geological series and locality. — Wood Bay series (lower Devonian), Mt Lyktan. Collected by A. HEINTZ in 1925.

Specimen no. 106 (pl. 16, fig. 2) consists of a portion of the dorsal side of rather large cephalic shield, preserved in part as in impression of the external surface. It shows quite well the polygonal areas of the external parts of the exoskeleton and that the outside of each polygonal area is provided with numerous, rather small closely and irregular set tubercles. The ornamentation of this specimen is thus exactly as in *C. höegi.*

Geological series, horizon and locality. — Wood Bay series (lower Devonian), Mt Lyktan. Collected by A. HEINTZ in 1925.

Specimen P. 550 (pl. 61, fig. 2) is the *Cephalaspis*-fragment figured by LANKESTER in 1884 (LANKESTER 1884, pl. II, fig. 5). It consists of the right cornu and an adjacent part of the cephalic shield preserved chiefly as impressions of the dorsal side. The external parts of its exoskeleton are subdivided into polygonal areas, each of which is provided with a rather big rounded tubercle. An ornamentation of this sort is not known in any of the *Cephalaspis*-species described above, and there is therefore much reason to believe that we are concerned here with a new species.

Geological series, horizon and locality. — Wood Bay series (lower Devonian), Mt Lyktan. Collected by A. G. NATHORST in 1882. (In the possession of the Riksmuseum of Stockholm).

Specimen no. 109 (pl. 61, fig. 1) consists of a fragmentary left cornu and an adjacent posterior part of the cephalic shield. As is seen from the figure given of it, it has a broad rather indistinctly defined pectoral sinus. The ornamentation is partly preserved and appears to consist of tubercles. While these tubercles are rather coarse and comparatively sparse on the dorsal side of the shield they seem to be rather fine and closely set, at least on the posterior parts of the ventral side of the cornua.

Geological series, horizon and locality. — Wood Bay series (lower Devonian), Mt Lyktan. Collected by O. HØEG in 1924.

Specimen no. 83 (pl. 5, fig. 3) consists of an anterior part of the ventral rim, exhibiting a tubercular ornamentation. The tubercles, which all are somewhat elongated, are considerably larger on the outer parts of the rim than towards the internal margin. Further it is worthy of notice that all the tubercles are arranged concentrically with the margins of the rim.

Geological series, horizon and locality. — Wood Bay series (lower Devonian). Ridge between Arla and Serla Glaciers. Collected by O. HOLTEDAHL in 1909.

Specimen no. 78 (pl. 40, fig. 1) consists of a small portion of the anterior part of a ventral rim, covered by a continuous superficial layer, which shows the usual pores and which in addition in the vicinity of the lateral border is thickened in places so as to form tubercles. More exactly, these tubercles, which are somewhat elongated, with their axes of length concentrically with the lateral border, are not irregularly scattered but arranged in transverse series in the very striking way shown in the figure cited. Since the ornamentation of the ventral rim is unknown in several of the new *Cephalaspis*-species established in this work, it is not possible to say whether the fragment of the rim dealt with here pertains to any of these species or whether it represents a new one.

Geological series, horizons and locality. — Red Bay series (Dovntonian). Lowest part of Mt Pteraspis. Collected by A. HOEL in 1912.

Specimen no. 79 (pl. 32, fig. 2) consists of a considerable part of a cephalich shield. But as this cephalic shield lacks the cornua and certain anterior parts, and in addition is badly fractured and affected by pressure, it is impossible to arrive at any certain opinion concerning its shape. It is from a rather small individual, the length probably not exceeding 4 cm. The interzonal part is somewhat extended backwards with its dorso-median portion and has a short obtuse elevation posteriorly on the dorsal side, an elevation which probably represented a vestigal small dorsal spine. The orbital openings are rather large. The dorsal electric field (*dsf*) is long and narrow. Somewhat anteriorly to its posterior end we find the opening of a small paired canal (d_1), which leads inwards to the big occipital vein sinus. This canal (d_1) and its functions have been dealt with in detail in the anatomical part of this work (cf. pp. 61—62, 86). The right lateral electric field (*lsf*) is well preserved in parts and appears to have been broad and welll developed. The character of the ornamentation is entirely unknown.

Whether this specimen represents a new species or whether it pertains to one of those already described above it is not possible to decide at present.

Geological series, horizon and locality. — Red Bay series (Downtonian); Mt Pteraspis, between summits 760 and 825. Collected by ADOLF HOEL in 1909.

Specimen no. 80 (pl. 35, fig. 4) is represented merely by a portion of the ventral rim. It is from an animal of about average size and is ornamented with numerous, small, somewhat elongated tubercles, which are arranged in lines concentrically with the lateral border of the rim. Thus the ornamentation resembles greatly that of the rim figured in pl. 5, fig. 3. The latter rim however, is, from another geological horizon than the one here under consideration.

Geological series, horizon and locality. — Red Bay series (Downtonian); in horizon *J* of Ben Nevis. Collected by ADOLF HOEL in 1909.

Specimen no. 87 consists of a part of a cornu and a adjacent small portion of a shield (pl. 43, fig. 3). The cornu was certainly in its original condition long and slender. It is provibed on the lower side with numerous rather coarse, irregularly scattered tubercles, which are somewhat lengthened.

Geological series, horizon and locality. — Red Bay series (Downtonian), Ben Nevis. Collected by A. HOEL in 1909.

Specimen no. 88 (pl. 33, figs. 2, 3) consists of certain parts of a left half of a rather small cephalic shield with a proximal part of the left cornu. In general shape the shield resembles that of *C. hoeli* and *C. gracilis* and may perhaps pertain to either of these species. Nothing is known concerning its ornamentation.

Geological series, horizon and locality. — Red Bay series (Downtonian), Ben Nevis. Collected by ADOLF HOEL in 1909.

Specimen no. 113 (pl. 43, fig. 4) consists of a small dorsal-part of a cephalic shield, a part which shows the small orbits and the nasal opening. As it is much weathered and abraded it has none of the ornamentation preserved. On the other hand, it displays beautifully the subdivision of the external parts of the exoskeleton into polygonal areas. It is not quite impossible that this specimen pertains to the same species as the specimen no. 77 (see pp. 283—284 above).

Geological series, horizon and locality. — Red Bay series (Downtonian). Horizon *F*, Ben Nevis. Collected by ADOLF HOEL in 1909.

Genus **Benneviaspis** n. g.

The genus *Benneviaspis* has been established for a new species from the Downtonian. With regard to its general characters the cephalic shield of this genus is rather suggestive of that in *Cephalaspis*. It differs, however, from that particularly in the development of the cornua, which do not reach backwards with their points beyond the interzonal part, and which in addition also issue rather much in a lateral direction. Moreover its postero-lateral angles are always somewhat produced, so that they reach further backwards than the posterior angle. With regard to the shape of the lateral electric field and the internal structures the genus appears to be closely related to *Hoelaspis*, *Boreaspis*, *Thyestes* and *Auchenaspis*. Among other things it may be mentioned that the canals for the first and second electric nerves to the lateral electric field remain united much farther antero-ventro-laterally than in *Cephalaspis*, that the canal for the n. trigeminus proper does not, as in *Cephalaspis*, pass between, but posteriorly to, the canals for the first two electric nerves to the lateral electric field, and that the canal for the dorso-lateral superficial vein 3 goes up to and unites with the canal for the capitis lateralis vein behind the orbit. In *Cephalaspis* the last-mentioned canal goes instead always to the postero-ventro-lateral corner of the orbit.

During a visit to the British Museum in February 1927 I discovered that a representative of this new genus occurs also in England, a representative which belongs to a second species for which I propose the name of *B. lankesteri* in honour of Sir R. LANKESTER (British Mus. Specimens P. 46568 and P. 46877. Both specimens have hitherto erroneously been referred to *Cephalaspis lyelli*). While the Spitsbergen species, which has been named *B. holtedahli*, comes from the Downtonian, the English species is from the Devonian, more exactly from Cradley near Malvern.

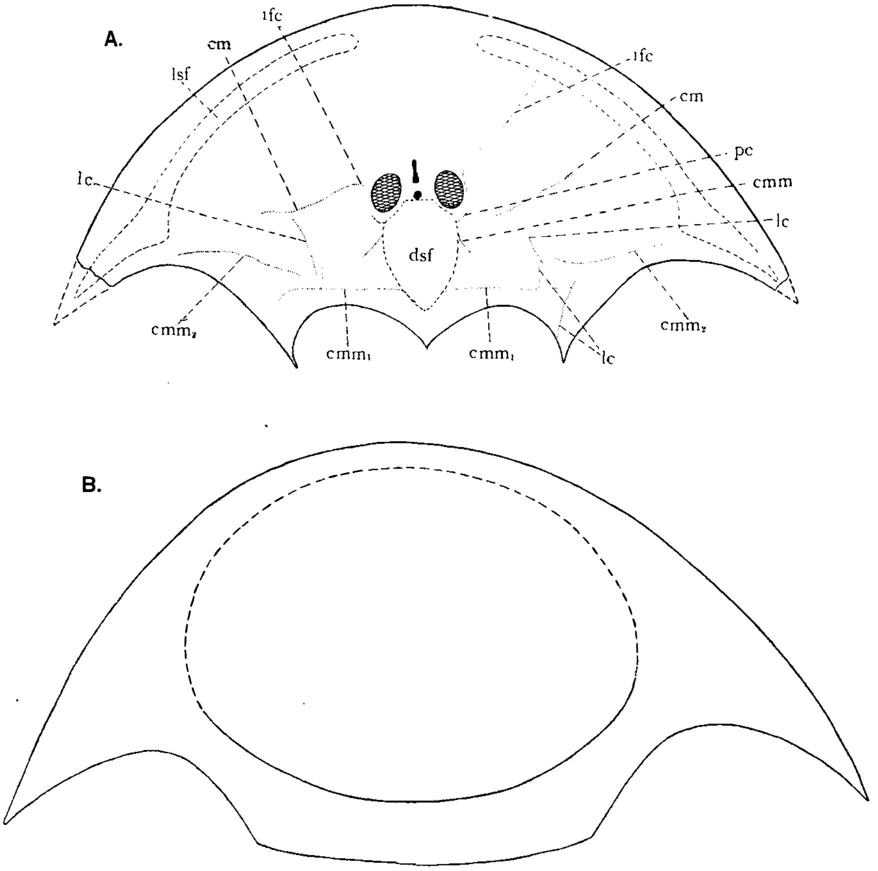
The genus *Benneviaspis* may be briefly characterized in the following way. Shield broad and flat. Cornua fairly well developed, issuing rather much in a lateral direction and never extending backwards beyond the posterior margin of the interzonal part. Pectoral sinus broad and comparatively shallow. Interzonal part broad with the postero-lateral angles produced so much that they reach farther backwards than the posterior angle. A paired lateral and an unpaired dorsal electric field, the former extending back on the cornu of its side but in additiion reaching with a postero-medial corner somewhat towards the shoulder-girdle. The common canal for two anterior electric nerves to the lateral electric field reaching to a point almost midway between the orbital opening and the lateral electric field. The canal for the n. trigeminus proper situated in its proximal part posteriorly to the common canal for the two anterior electric nerves to the lateral electric field; in its distal part, on the contrary, posteriorly to the canal for the second one of these electric nerves. The canal for the dorso-lateral superficial vein 3 passing up to, and uniting with the canal for the capitis lateralis vein close behind the orbit. Body unknown.

21. *Benneviaspis holtedahli* n. sp.

(Pls. 41, 42; pl. 43, fig. 1; text-fig. 76).

This species is preserved by four more or less imperfectly preserved cephalic shields (specimens no. 70—72, 74). As a holotype I have chosen the one figured in pl. 43, fig. 1 (specimen no. 70).

The holotype is 3,4 cm. long from the rostral margin to the posterior angle, about 7 cm. broad between the posterior ends of the cornua, and about 0,5 cm. high close anteriorly to the posterior angle. It seems, however, to be somewhat flattened by pressure in the rock, so that it may probably have been a little higher than in its present state of preservation. The other shields (no. 71, no. 72 and no. 74) are approximately of a similar size as the holotype.



Text-fig. 76. *Benneviaspis holtedhali* n. sp.
Restoration of cephalic shield. *A*, from the dorsal side chiefly after specimen no. 70. The lateral line system of grooves after specimen no. 71. *B*, from the ventral side after specimen no. 72. A, about 4/3, and B, a little less than 3/2 of the nat. zise.
cm, groove perhaps corresponding to the preopercular of jugal canals of fishes; *cmm*, groove, probably corresponding to the middle head line of pit organs of fishes; $cmm_1 + cmm_2$, groove corresponding either to the posterior head line of pit organs or to the supratemporal commissure of fishes; *dsf*, dorsal electric field; *ifc*, infraorbital groove; *lc*, cephalic division of the main lateral line; *lsf*, lateral electric field; *pc*, groove corresponding to the suprapineal canal of *Pteraspis* and to the suprapineal lateral line organs in Petromyzontids.

With regard to general shape the cephalic shield of the species in question is, as is evident from the measurements given, very broad, its breadth being more than twice the length. It is further noticeable that it is rather low.

The rostral margin exhibits hardly any traces of a rostral angle. The cornua, which are broad and short and much flattened in a dorsiventral direction, project much laterally and do not reach backwards beyond the interzonal part. Their medial and lateral margins are devoid of denticles. The pectoral sinus is shallow and broad and not very distinct. The interzonal part is broad and without dorsal spine and reaches backwards behind the cornua. Its postero-lateral angles are produced rather much backwards and are longer than the posterior angle. They also reach backwards beyond the point of that angle.

The posterior margin of the dorsal half of the interzonal part between the posterior angle and each lateral angle is rather deeply concavated. The orbits, which are oval in shape, with the longitudinal axes parallel or converging forwards, lie behind the middle of the length of the shield and thus rather far back. The dorsal electric field is short and broad, its maximum breadth, which is situated in the anterior half, constituting more than one half of the length. There is no median ridge between it and the posterior angle. The lateral electric field is well developed and continuous and reaches far back on the cornu of its side; and moreover it is characterized by the presence of a distinct medial corner which just in front of the cornu projects somewhat medially on the shoulder girdle. The oralo-branchial fenestra is broader than it is long.

The superficial layer of the exoskeleton is continuous and entirely smooth but with the usual pores perforating it. There are no traces of polygonal areas.

The sensory canal system is seen in one of the specimens (no. 71) and is as shown by text-fig. 76 A (cf. pp. 235—239 above). Also several internal structures are exhibited in certain of the specimens (pls. 41, 42).

Remarks. — This species, which I have named in honour of Professor O. HOLTEDAHL, of Oslo, who was a member of several of the Norwegian expeditions (1909—1911) during which the material described in this memoir was collected, is very easely distinguished from the English species (*B. lankesteri*) by the greater breadth of its cephalic shield, by the more broad and strongly developed cornua and by the different shape of the electric fields.

Geological series, horizon and locality. — Red Bay series (Downtonian). Horizons *J*, *L* and the Cliff at Ben Nevis. Collected by ADOLF HOEL in 1909.

Genus **Hoelaspis** n. g.

With regard to the internal structures this genus appears to be closely allied to *Benneviaspis*, *Boreaspis*, *Thyestes* and *Kiaeraspis*. Thus it has the canals for the two most anterior nerves to the lateral electric field united with each other at least as far as midway between the said electric field and the orbit. Moreover, in it the canal for the n. trigeminus proper lies behind the canals for the two anterior nerves to the lateral electric field, and the canal for the dorso-lateral superficial vein passes up to and unites with the canal for the capitis lateralis vein behind the orbit. Finally it may be added that, as in *Benneviaspis* and *Boreaspis*, the lateral electric field extends backwards on the cornu of its side but that in addition it has in its posterior part a short medial corner or process which issues in a medial direction. The most important characters by which it is separated from other allied genera are the development and direction of the cornua and the absence of a distinct pectoral sinus.

A diagnosis of the genus would be as follows. Cephalic shield broad and low with a small but distinct rostral process. Cornua long and rather robust, and directed straight laterally or laterally and slightly anteriorly. Pectoral sinus shallow and not distinctly defined. Interzonal part short and broad. A paired lateral and an unpaired dorsal electric field, the former with a distinct postero-medial corner on the medial side just medially to the cornu of its side. The canals for the two anterior nerves to the lateral electric field united at least as far forwards as midway between this field and the orbit. The canal for the n. trigeminus proper situated with its proximal part behind the common canal for the first and second electric nerves to the lateral electric field, with its distal part, on the contrary, behind the canal for the second of these two nerves. The canal for the dorso-lateral superficial vein 3 passing up to and emptying into the canal for the capitis lateralis vein behind the orbit. Body unknown, but, so far as can be judged, probably rather flattened in a dorsi-ventral direction.

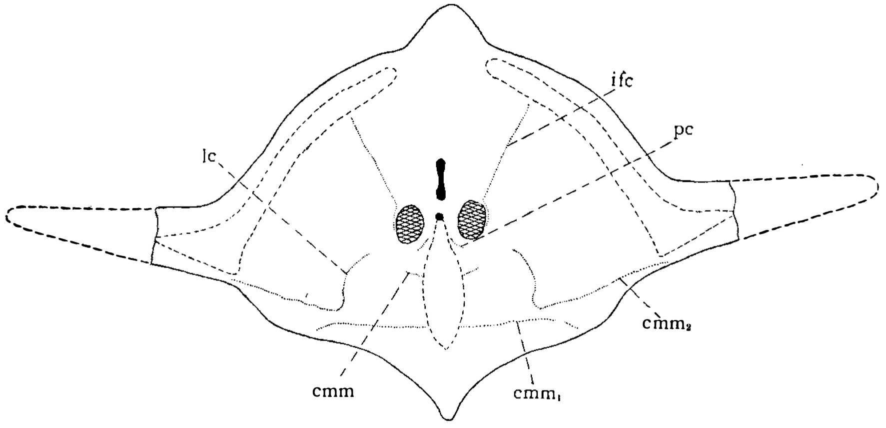
The genus is based only on a single species from the Spitsbergen Downtonian and has been named in honour of Docent ADOLF HOEL of Oslo for his great merits in the exploring of the geology of Spitsbergen.

22. *Hoelaspis angulata* n. sp.

(Pls. 44—46; pl. 47, fig. 1; text-fig. 77).

The material available of this species consists of nine more or less imperfect cephalic shields (specimens nos. 73, 89—95, 105). As a holotype for the species I have taken a very well preserved shield (specimen no. 89, pls. 44, 45), which lacks the distal parts of the cornua.

In the holotype the length, measured from the tip of the rostrum to the posterior angle, is 1,45 cm., while the breadth, taken between the posterior ends of the imperfect cornua, amounts to 2 cm. But as the cornua must have been much longer, the total breadth between their distal ends may by estimated at at least 3,6 cm. The height of the holotype is 0,25 cm. only. The majority of the other shields are of about a similar size or smaller than the type and it is thus obvious that the species was small.



Text-fig. 77. *Hoelaspis angulata* n. sp.
Restoration of cephalic shield. After specimens no. 89, 90, 92 and 93, lateral line system after specimen no. 73. 4/1.

cmm, groove perhaps corresponding to the middle head line of pit organs in fishes; $cmm_1 + cmm_2$, transversal groove (in two pieces) corresponding to either the posterior head line of pit organs or to the the supratemporal commissure of fishes; *ifc*, infraorbital groove; *lc*, cephalic division of the main lateral line; *pc*, groove probably corresponding to the suprapineal groove of Pteraspids and the suprapineal lateral line organs of Petromyzontids.

As is seen from measurements given, the shield is rather broad and flat. The rostral part is somewhat prodused into a short and rather broad rostral process. Between the rostral process and the cornu the lateral border exhibits an obtuse but rather distinct angle. The cornua, which are directed straight laterally or laterally and somewhat anteriorly, are rather strongly developed and long, but are not preserved in their full length in any of the specimens available. Concerning their shape it is further to be noticed that they are flattened in a dorsi-ventral direction. So far as can be judged, they are entirely devoid of denticles. The pectoral sinus is shallow and indistinctly bounded. The interzonal part is broad and short with a pronounced posterior angle, without dorsal spine, and without median longitudinal ridge. Postero-lateral angle much rounded off. The orbits, which lie slightly behind the middle of the distance between the tip of the rostral process and the posterior end of the posterior angle, are oval in shape and have their longitudinal axes almost parallel, or perhaps slightly diverging forwards. The dorsal electric field is rather long and narrow, its breadth being contained more than twice in the length. And it should be added that it seems to be rather narrow in its anterior third. The lateral electric field is rather narrow in its larger anterior part, but widens somewhat in its posterior part, which extends laterally on the cornu of its side for some distance, but certainly not more then to about the middle. On the posterior part of the medial side the last mentioned electric field has a pronounced corner or process, which projects towards the shoulder-girdle.

As is shown by the plates (pls. 44—46; pl. 47, fig. 1), the holotype, and also several of the other specimens display very well several of the cavities and canals of the interior of the head. It is thus easely seen (pl. 45) that the first (sel_1) and second (sel_2) canals to the lateral electric field, the canal for the trigeminus proper (V_2) and the canal for the dorso-lateral superficial vein 3 ($v. ls_3$) are as in *Benneviaspis*, *Boreaspis* and *Kiaeraspis*, and not as in *Cephalaspis*.

The superficial layer of the exoskeleton is continuous and smooth, but with the usual pores. There are no indications whatever of polygonal areas.

Geological series, horizons and locality. — Red Bay series (Downtonian). Horizons *J*, *K*, *L*, *O*, at Ben Nevis. Collected by ADOLF HOEL in 1909.

Genus **Boreaspis n. g. and certain remarks on Thyestes** EICHWALD.

This new genus is clearly allied to *Benneviaspis*, *Hoelaspis*, *Thyestes* and *Kiaeraspis*, aggreeing with these genera with regard to the type of the lateral electric field, the relations of the two anterior nerve canals to that field, and the position of the canal for the n. trigeminus proper. In addition it deserves to be mentioned here that as regards the general shape of the cephalic shield it is even specially suggestive of *Thyestes*. It is characterized as a genus of its own by the presence of a very long rostral process, by the slenderness of the cornua and by its peculiar development of the lateral electric field.

A definition of the genus, so far as it is known up to now, would be as follows. Cephalic shield with a very long rostral process. Cornua slender and rather weak, issuing in a postero-lateral direction and not reaching as far backwards as beyond the interzonal part. Pectoral sinus distinct and rather deep. Interzonal part relatively long and broad. Lateral electric field extending only very slightly backwards on the cornu, but with a medial corner in its posterior part, a corner which is much enlarged so that it extends postero-dorso-medially across the shoulder-girdle on to the antero-lateral portion of the interzonal part of the shield. The canal for the first and second electric nerves to the lateral electric field fused with each other almost as far latero-ventrally as to the medial margin of the lateral electric field. Canal for the n. trigemenius proper situated behind the common canal for the two first nerves to the lateral electric field. The relations of the canal for the dorso-lateral superficial vein 3 unknown.

In this connection a few remarks may also be given on the genus *Thyestes*. And there is the more reason to enter upon that genus since its conception has hitherto not been quite definitely defined.

The genus *Thyestes* was etablished in 1854 by EICHWALD (pp. 108—110) for a small Cephalaspid from Oesel. Although EICHWALD's description and figure are not only imperfect but in certain points inaccurate too they are, however, certainly sufficiently good to render possible a recognition of the genus. PANDER in 1856, in his monograph on the fishes of the Silurian system, was the next writer that dealt with *Thyestes* and published new and better figures of it. The genus was, however, not considered by PANDER to be an independent one, but the genotype was referred by him to *Cephalaspis*. Further contributions to the knowledge of the genotype were published by EICHWALD in 1860 (pp. 1532—1533), by SCHMIDT in 1866, by ROHON in 1892 (pp. 13—37), 1895 (pp. 16—61) and 1896 (1896 a, 1896 b, pp. 223—234) and finally by JAEKEL in 1911 (p. 35, fig. 20).

In 1857 EGERTON etablished the genus *Auchenaspis*, which later on appeared to resemble *Thyestes* so much (cf. WOODWARD, 1891 a, pp. 195—196) that it is generally concidered by several recent writers to be identical with this. According to current rules of nomenclature the name *Thyestes* would therefore replace *Auchenaspis*. Nevertheless especially in the English palaeoichthyological literature the latter name has often been preferred.

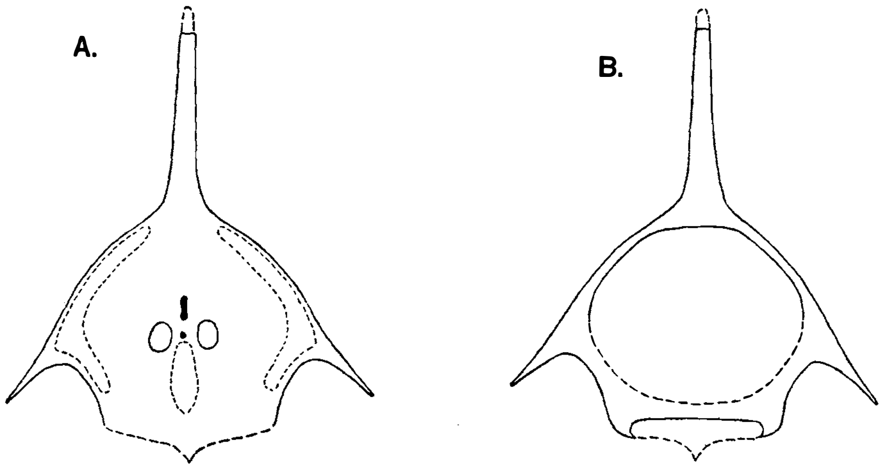
I myself am also of the opinion that there are no differences of generic importance between the cephalic shields of *Thyestes verucosus* — the genotype of *Thyestes* — on the one hand, and *Auchenaspis salteri* and *Auchenaspis egertoni*, on the other; and accordingly I have adopted the name *Thyestes* as the generic name for all these three species. Whether, on the contrary, the species known as *Cephalaspis schrencki*, which was referred to *Thyestes* by SCHMIDT in 1894, really pertains to *Thyestes* or represents a genus of its own is impossible to decide with certainty at present, as it is still too imperfectly known. A figure of a fragment of a shield of this species is shown in pl. 48, fig. 2.

23. *Boreaspis rostrata* n. sp.

(Pls. 13—15; text-fig. 78).

The material available of this species consists of two cephalic shields (specimens nos. 96, 97), the most complete of which (specimen no. 96, pls. 14—15, text-fig. 78) has been chosen as a holotype.

The holotype is about 1,5 cm. long from the anterior end of the rostral process to the posterior border of the interzonal part. Its breadth is about 1,4 cm. between the posterior ends of cornua, while the heigth



Text-fig. 78. *Boreaspis rostrata* n. sp.
Restoration of cephalic shield. *A*, in dorsal, *B*, in ventral view. Magnification about 3/1.

at the posterior end of the interzonal part probably amounts to 0,35 or 0,4 cm. The second specimen (no. 97) seems to have been almost twice as large the holotype, but on account of its imperfect state of preservation no exact measurements can be obtained.

The general shape of the field is seen in text-fig. 78. The rostral part is produced into a long narrow rostral process, which in the holotype, in which it is most complete, is almost as long as the shield; but as even in the holotype it is not present in its entirety it must have have been still somewhat longer. The cornua, which are directed postero-laterally, are rather weak and slender and do not reach backwards as far as does the interzonal part. As far as can be seen, their medial margin is without denticles. The pectoral sinus is distinct and rather deep. The interzonal part is broad and rather long. The orbital openings are fairly small with their longitudinal axes almost parallel or slightly converging forwards. The dorsal electric field is probably rather narrow in relation to its length. The lateral electric field is well developed but reaches only very slightly backwards on the cornu of its side. Instead the medial corner of its posterior part is much enlarged and developed into a postero-medial portion of the field, a postero-medial portion which extends across the shoulder-girdle on to the most antero-lateral portion of the interzonal part of the shield.

The endoskeleton of the shield is completely ossified, consisting of a cancellous bone (pls. 14, 15), lined by periostal bone-layers on the exposed surfaces and in all cavities and canals. In other forms known it is much less ossified, its ossification consisting in the main solely of thin bone-layers on its exposed surfaces and thin bone-layers lining the cavities and canals, while its interior was made up of an uncalcified rather solid tissue, probably muco-cartilage. The cranial cavity, the labyrinth cavity with the divisions for the semicircular canals, several canals for nerves and certain other structures are rather well displayed (pls. 13—15). Special interest attaches to the fact that the common canal ($sel_{1,2}$) for the first two electric nerves to the lateral electric field reaches undivided down to the medial margin of the lateral electric field and that the canal (V_2) for the trigeminus proper throughout its length lies posteriorly to the preorbital portion of that common canal for the two anterior electric nerves to the lateral electric field. It should further be mentioned that the postbranchial wall (*p. brw*, pls. 14, 15) is well shown and that, as in *Kiaeraspis*, the foramen for the oesophagus (*oes*) and that for the truncus arteriosus (*tr*) are separated from each other. Finally a considerable part of the marginal vein sinus and the marginal vein canal are clearly seen (*vs. marg*, *v. marg*, pl. 15). The oralo-branchial fenestra is slightly broader than long (text-fig. 78).

The development of the superficial layer of the exoskeleton is entirely unknown. There are probably no traces of polygonal areas.

Geological series, horizon and locality. — Wood Bay series (lower Devonian), probably not very high above the Downtonian, W. of the Hoffnung Glacier. Collected by G. WATNELIE in 1910.

Genus **Kiaeraspis** n. g.

This genus is in all its chief characters allied to *Benneviaspis*, *Hoelaspis*, *Boreaspis* and *Thyestes*, most closely, however, to *Boreaspis* and *Thyestes*. It is chiefly characterized by its very long interzonal part, which seems to consists of about twice as many segments as that in *Boreaspis* and *Thyestes*, and by its strickingly short, broad cornua. Attention deserves also to be called to the fact that with regard to general shape it is suggestive of *Didymaspis* too, which, as shown by text-fig. 80, has a very long interzonal part and short vestigal cornua, and that in fact it appears to represent a transitional form between ordinary Cephalaspids and *Didymaspis—Tremataspis*.

The characters of the genus my be summarized as follows. Cephalic shield, as a whole, strikingly long, much longer than broad. Cornua broad and very short, issuing in a lateral and only slightly posterior direction. The pectoral sinus narrow, shallow and very indistinct. Interzonal part very strongly developed, consisting of about 9 segments and constistuting about one half of the total length of the shield. One lateral paired and one dorsal unpaired electric field; the former with a strongly developed postero-medial corner extending postero-dorso-medially on the shoulder-girdle. The common canal for the two first nerves to the lateral electric field extending undivided to the medial margin of the lateral electric field, so that in fact there are only five nerve canals entering that electric field. The canal for the n. trigeminus proper situated behind the preorbital portion of the common canal for the two anterior nerves to the lateral electric field. The dorso-lateral superficial vein 3 passing up to and uniting with the canal for the capitis lateralis vein just behind the orbit. The anterior part of the body rounded pentagonal in shape.

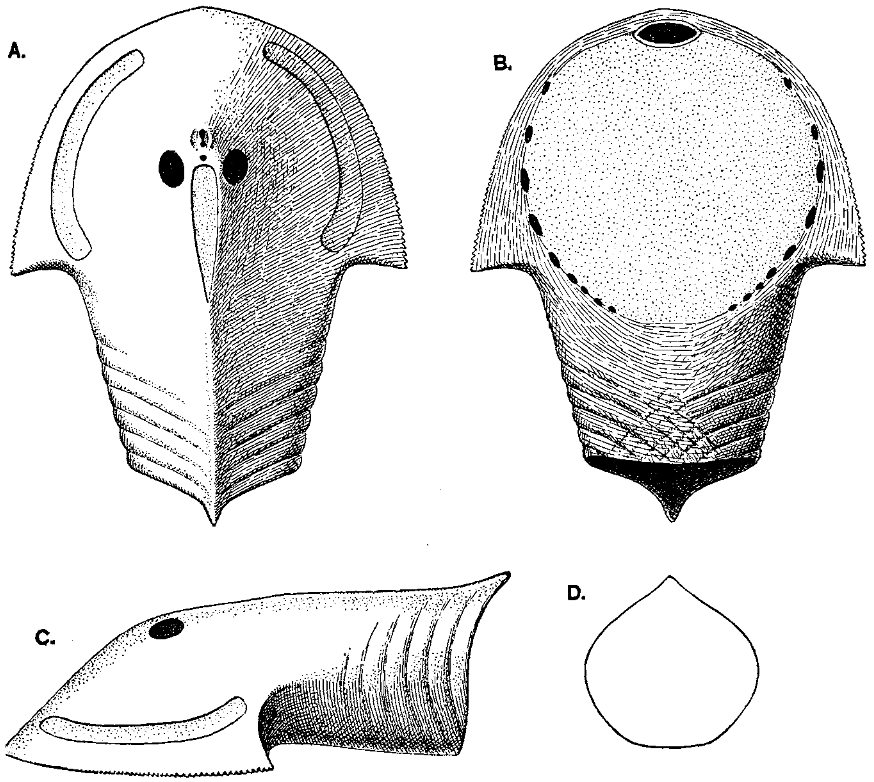
24. *Kiaeraspis auchenaspidoides* n. sp.

(Pls. 49—58; text-fig. 79).

This species is represented by eigth more or less complete cephalic shields (specimens nos. 98—104, 107). As a holotype I have chosen shield no. 98, which is fairly complete (pl. 53; pl. 54, fig. 2; pl. 55).

All the shields are small, their dimensions being as follows: length from the rostral angle to the posterior angle: 1,4—2,1 cm.; maximum breadth (between the tips of the cornua) 1,2—1,8 cm.; and height in the posterior portion of the interzonal part (anteriorly to the dorsal spine) 0,8—1,4 cm.

The shield (text-fig. 79) is considerably longer than it is broad. Anteriorly it has a rather distinct rostral angle. The cornua, which issue in a lateral and slightly posterior direction, are broad and very short. The pectoral sinus is shallow and indistinctly bounded, indicating that the pectoral fin was rather small. The interzonal part is characterized by both a great width and a great length, the length being even so considerable that is constitutes about one half of the entire length of the shield. It is provided with a low dorsal spine, from which a distinct median dorsal ridge continues forwards for some distance, probably to the posterior end of the dorsal electric field. It is further of much interest that the interzonal part shows indications of five, and in certain exceptional cases of six segments in its posterior half (text-fig. 79). And under the assumption that the segments in the anterior half were of a similar breadth it would obviously be composed of a least 9 segments. The most posterior segment is always imperfect ventrally as the scales belonging to it there have not coalesced with the shield but retain their independence. Accordingly the interzonal part is one segment shorter ventrally than it is dorsally. Concerning the interzonal part it deserves further to be mentioned that its ventral wall on the outside still shows distinct traces of the small scales by the fusion of which it was formed. The orbital openings are oval, with the longitudinal axes parallel or slightly diverging forwards. The dorsal electric field is imperfectly preserved in all the shields available, and its exact shape is therefore not known. As far as can be made out, however, it seems to have been rather long (text-fig. 79). The lateral electric field is well developed, but does not reach backwards on the cornu. Instead it has like in *Boreaspis* the part corresponding to the medial corner of *Benneviaspis* and *Hoelaspis* rather much enlarged and



Text-fig. 79. *Kiaeraspis auchenaspidoides* n. sp.
Restoration of cephalic shield. *A*, in dorsal view, *B*, in ventral view, *C*, in lateral view, and *D*, in transverse section (near the posterior end of the interzonal part). Chiefly after the holotype (specimen no. 98). 3/1.

extended postero-dorso-medially on the shoulder-girdle. The oralobranchial fenestra is of a rather circular shape.

As is well shown by the plates (pls. 49—58) the cephalic shield of this species is very well preserved with regard to internal skeleton, cavities and canals etc. All of these internal structures have been fully dealt with in the anatomical part of this monograph. Here however, attention should be called to the fact that the common canal ($sel_{1,\,2}$) for the two most anterior nerves to the lateral electric field does not divide into two until at or very close to the very entrance into the said electric field, and that therefore in fact only five canals for nerves pass down to that field. The canal for the n. trigeminus proper (V_2) and the canal for the dorso-lateral superficial vein 3 were exactly as in *Benneviaspis*, *Hoelaspis* and *Boreaspis*.

The development of the superficial layer of the exoskeleton is unknown. The anterior and lateral borders of the shield from the vicinity of the rostral angle to the point of the cornua are provided with a series of small tubercles, which on the lateral margins of the cornua are somewhat enlarged, forming there small posteriorly curves denticles. Otherwise nothing is known with certainty of the ornamentation. There are no traces whatever of polygonal areas.

Immediately behind the postbrancial wall, and thus in the anterior end of the interzonal part, the trunk was broader than it was high. Farther backwards its width gradually decreases, so that at the posterior end of the interzonal part it was roundedly pentagonal or almost circular (text-fig. 79 D). As far as can be judged from the posterior portions of the interzonal part, the division of the body following behind the cephalic shield was covered by high narrow scales on the lateral sides and by small more and less lozenge-shaped scales on the ventral side.

Geological series, horizon and locality. — Red Bay series (Downtonian). Horizons *J* and *L*, Ben Nevis. Collected by ADOLF HOEL in 1909.

REMARKS ON CERTAIN OTHER FORMS

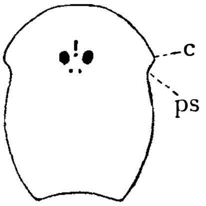
The detailed knowledge now gained of the *Cephalaspidae* by the study of the wonderfully preserved Spitsbergen material helps in several respects to throw light on the organization of the *Tremataspidae*, the *Anaspida*, the *Heterostraci*, the *Cyclostomata* and *Palaeospondylus*; and I have therefore found it suitable to give here a brief account of all these forms and to compare them with and discuss their affinities to the *Cephalaspidae*. In addition I have found it appropriate to add here a few remarks on the *Arthrodira* and *Antiarchi*.

Family Tremataspidae.

The family *Tremataspidae*, as pointed out above (pp. 9—15), was established by Woodward (1891 a, p. 201) for the genus *Tremataspis*, which until now has been the by far best known genus among the *Osteostraci* (cf. Rohon 1892, pp. 37—88; 1894; Patten 1903 a; 1912, pp. 290—292, 359—363; Jaekel 1903, pp. 84—93; 1911, p. 34; 1919, pp. 235—239; Wiman 1918, pp. 84—95). Rohon (1896 a, pp. 15, 29) and Zittel (1895, p. 554) placed (cf. p. 3 above) *Didymaspis* too in the family *Tremataspidae*, but this procedure has not been followed by other palaeoichthyologists.

Tremataspis is, as we know, provided with a cephalic shield which in most respects is very similar to at in the *Cephalaspidae*, but which, however, differs from that by the presence of a longer interzonal part, by the absence of cornua and pectoral sinus and by a somewhat different minute structure. It should be noticed here, however, that among the *Cephalaspidae* there are such forms as *Kiaeraspis* which, both with regard to the length of the interzonal part and with regard to the slight development of the cornua and pectoral sinus, show a decided tendency to an evolution in the direction towards *Tremataspis*. And since in addition such a form as *Didymaspis* has been found, which has the interzonal part approximately as long as in *Tremataspis* and which has only faint traces of cornua and pectoral sinus (text-fig. 80; cf. also p. 28 above), it is quite clear that with regard to the backward extension of the interzonal part and the reduction of the cornua and pectoral sinus there are almost all transitional stages between the typical *Cephalaspidae* and *Tremataspis*.

The absence of cornua and pectoral sinus indicates that *Tremataspis* had no homologues of the pectoral fins of the *Cephalaspidae*. As we shall see, it is evident that several groups of the Ostracoderms had pectoral fins or structures derived from these. And it seems not improbable therefore that pectoral fins or structures homologous with these originally were present in all Ostracoderms or at least in the majority of them. Since this is the case, and since the cephalic shield of *Tremataspis* obviously includes a shoulder-girdle part homologus with that in the *Cephalaspidae*, there is in my opinion strong reason to believe that the absence of cornua, pectoral sinus and pectoral fins in *Tremataspis* is a secondary condition arisen from a *Cephalaspis*-like one and not the reverse, as one perhaps would have been inclined to think. Or expressed in another way: there seems to be much evidence in favour of the view that the cornua, the pectoral sinus and the pectoral fins have been entirely reduced in *Tremataspis*.



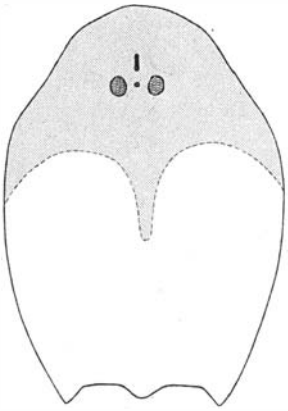
Text-fig. 80. *Didymaspis grindrodi*. Schematic sketch, showing the approximate appearence of the cephalic shield in dorsal view. *c*, cornu; *ps*, pectoral sinus.

The difference in minute structure between the exoskeleton of *Tremataspis* and that of the *Cephalaspidae* has already been dealt with to a certain extent above (pp. 38—40), and, as was especially pointed out, it appears on a detailed analysis to be much less than at the first glance. In fact, it is so insignificant that we must imagine the exoskeleton of *Tremataspis* and that of the *Cephalaspidae* to have arisen from a common type of structure; but whether this common type of structure was more as in *Tremataspis* than as in the *Cephalaspidae* or the reverse it is difficult to say at present. In this connection it deserves to be pointed out that the minute structure of the exoskeleton of *Didymaspis* is unknown so far.

As was evident already from the paper published by WIMAN in 1918 (pp. 84—95), the cephalic shield of *Tremataspis* has, like that in the *Cephalaspidae*, an extensive endoskeletal component. The extension of this component when seen from above was about as shown in text-fig. 81, and we thus find that it had a long occipital region and that it greatly resembled that in the *Cephalaspidae*, particularly that in *Kiaeraspis*. It was made up of cartilage, which was provided with thin perichondral layers of bone on all exposed surfaces and within all cavities and canals (cf. pl. 47, fig. 2; pls. 59, 60) and accordingly it was in this respect too as in most *Cephalaspidae*. Just as in these too, it was composed of endocranial, visceral and shoulder-girdle components, the last of which has already been referred to above. Of these components we will first consider the endocranial one, or as we shall call it here simply, the endocranium.

The endocranium is badly preserved in the specimens in which I have had the opportunity of studying it (pl. 47, fig. 2; pls. 59, 60); and I am therefore not in position to enter upon more of it than the cavum cerebrale cranii, the labyrinth cavity, the orbit and certain canals.

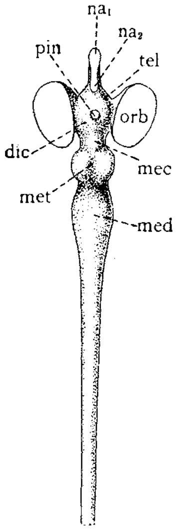
The cavum cerebrale cranii is best shown in the specimen figured in pl. 59 (which is the specimen described by WIMAN in 1918); but certain parts of it are also seen both in the specimen shown in pl. 47, fig. 2 and in that reproduced in pl. 60. As is fully clear from these specimens, it is in the fossil condition, just as in the *Cephalaspidae*, in open communication anteriorly with an ethmoidal cavity which opens anteriorly by means of the nasal aperture, which, as we know, is typically Cephalaspid-like in shape. Further it is easy to see that with regard to both general shape and subdivisions it differs from that in the *Cephalaspidae* only in certain details of minor importance, such as greater length of the division for the medulla (*med*) and cerebellum (*met*) respectively. The shape of its divisions in detail is elucidated by the plates quoted and by text-fig. 82.



Text-fig. 81. *Tremataspis schmidti.* Sketch showing the approximate shape and extent of the endoskeletal component (shaded) of the cephalic shield indorsal view.

In this connection attention should be called to the circumstance that the interpretation given by WIMAN in 1919 of the cavum cerebrale and its divisions is incorrect in many respects. That this is the case, however, is easily understood if we realize that at that time nothing was known concerning the places of exit of the cranial nerves and that consequently there was no reliable basis for a judgement as to the position of the different divisions of the brain within the divisions of the cavum cerebrale cranii. I shall not enter here upon all the mistakes made by WIMAN, but I should like to point out that what he considered to be the division for the mesencephalon is in fact the division for the cerebellum, that the division which he thought to have lodged the diencephalon appears to be the division for the mesencephalon, and that there is no evidence whatever that the division for the medulla was as broad as in his restoration but instead that it was as in the *Cephalaspidae* (text-fig. 82).

As pointed out by WIMAN, the cavum cerebrale cranii is in the fossil condition by means of a wide fenestra optica in cummunication with the orbit of each side. In the specimen figured in pl. 60 there is seen a rather fine canal, which goes from the antero-dorsal part of the division for the cerebellum to the postero-medial part of the orbit.



Text-fig. 82. *Tremataspis schmidti.* Outlines of a cast of the cavum cerebrale cranii in dorsal aspect. Restoration based on the specimens figured in pl. 47, fig. 2 and pls. 59 and 60.

dic, division for the diencephalon; *mec*, division for the mesencephalon; *med*, division for the medulla oblongata; *met*, division for the cerebellum; na_1, na_2, anterior and posterior divisions of nasal aperture (the anterior one for the hypophysial sac); *orb*, orbit; *pin*, pineal opening and canal; *tel*, division for the telencephalon.

This canal (*a. dsm*) may have transmitted either the n. trochlearis or, more probably, a branch of the postorbital superficial artery.

The labyrinth cavity is like the cavum cerebrale cranii imperfectly preserved in the specimens available (pl. 47, fig. 2; pls. 59, 60), its most dorsal and lateral parts having in these specimens been destroyed either by weathering or by unfavorable conditions before and after the process of fossilization. What is found preserved of it is a part of a big vestibular division (*vest*) and a part of a commissural division, which are both very suggestive of the corresponding ones in the *Cephalaspidae* and which both indicate that the labyrinth cavity as a whole probably must have been very much as in these.

From the dorso-medial part of the labyrinth cavity there issues, as in the *Cephalaspidae*, a wide canal (*des*, pl. 47, fig. 2; pl. 59) for the electric nerve to the dorsal electric field, a canal which in all respects seems to be exactly as in the *Cephalaspidae.* Thus it passes off dorso-medially, dorsally to the most anterior part of the division of the cavum cerebrale cranii for the medulla and close behind the division of the same cavity for the cerebellum. Further it is distinctly seen (pl. 47, fig. 2) that it meets and unites with its fellow of the opposite side within the most basal part of the dorsal electric field. From the posterior side of the canal in question a second canal (*v. dsv*, pl. 47, fig. 2) is given off backwards. This latter canal which is given oft wackwards evidently corresponds to the one in the *Cephalaspidae* that transmitted the supposed otical vein. As in the Cephalaspids, it certainly led backwards to the occipital vein sinus. And by means of that it seems to have communicated with the canal *d. end* (text-fig. 83; pl. 47, fig. 2), which opens on the dorsal side of the shield somewhat postero-laterally to the dorsal electric field and which quite certainly corresponds to the canal d_1 of the Cephalaspids. Since the canal *d. end* in this case cannot have been a vein canal, the opinion advanced by most earlier writers (ROHON 1892, p. 69; 1894, p. 208; 1896 a, fig. 7, on p. 28 etc.; JAEKEL 1911, fig. 19; WIMAN 1919, p. 90; etc. etc.) that it would have lodged the ductus endolymphaticus seems very likely. Accordingly there seems to be much reason to believe that the ductus endolymphaticus was of a considerable size and that it extended from the labyrinth cavity through the canal *v. dsv* for the supposed otical vein, and further through the occipital vein sinus and the canal *d. end* up to the dorsal surface of the shield. From the ventro-lateral part of the vestibular division of the labyrinth cavity several canals for electric nerves to the lateral electric fields issue in a latero-ventral direction. These canals, a few of which are shown in pl. 60 (sel_a, sel_m, sel_p), are arranged in two groups, an anterior group which supplied the anterior lateral electric field and which consisted of two or three canals, and a posterior group which supplied the posterior lateral electric field and which consisted also of two or perhaps three canals. The total number of canals to the lateral electric fields was thus at least four and can not have exceeded six. To give their number more exactly than that is not possible, but it is nevertheless fully evident that the conditions with regard to the nerves to the lateral electric fields were not very different from those in the *Cephalaspidae.*

A part of the canal for the vena capitis lateralis (*v. cl*, pl. 60), stretching from the orbit and backwards for some distance, is preserved in one of the specimens studied by me.

Concerning the orbits little can be said here because of the fact that in the material available to me they are very imperfectly preserved. It should therefore only be pointed out here that in all respects they seem to have been developed in much the same way as in the *Cephalaspidae.*

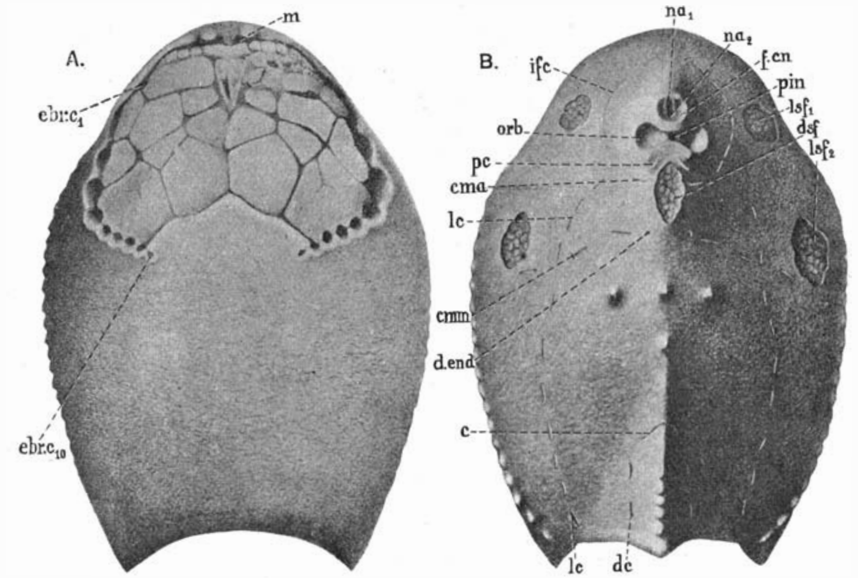
The visceral part of the endoskeletal component of the cephalic shield — or, as it will simply be termed here, the visceral endoskeleton — is developed in a similar way as in the Cephalaspids, and, as in them, it bounds, together with the endocranium, a very extensive oralo-branchial chamber. The transverse septum (*p. brw*) which has been observed by several writers behind the otic region, and which is partly shown in horizontal section in pl. 59, is nothing else but the postbranchial wall, that is to say, the part of the visceral endoskeleton that bounds the oralo-branchial chamber posteriorly.

On the lateral and posterior surface of the oralo-branchial chamber there are found distinct traces of branchial fossae (k, k_1—k_4, pls. 59, 60) of a similar type to those in the *Cephalaspidae*, and in addition there seem also to have been canals for ventral transversal superficial veins as in the *Cephalaspidae* (*v*, pl. 60). How many the branchial fossae were cannot be ascertained on the material available to me, but as far as can be judged from the number of external branchial openings observed by PATTEN (1903 a, pl. 2, fig. 8), they would seems to have been 10 (text-fig. 83) as in at least the majority of the *Cephalaspidae.* And if PATTEN'S restoration is reliable in this respect as seems to be the case, the branchial fossae would also with regard to mutual size and position have been very mush as in the *Cephalaspidae.*

The lateral line system of the dorsal side of the cephalic shield was accurately described by PATTEN in (1903 a, pp. 20 - 22), but PATTEN did not discuss either its mode of innervation or its homologues; nor has this been done later on either by himself or by anybody else. On account of this it may here be of interest to deal with it in detail. As is well known, it consist of shallow, narrow grooves which are situated in the superficial layer and consequently in such a way that they have a very superficial position. The grooves are mostly not continuous throughout their extent but subdivided in a fairly regular way into rather short pieces (text-fig. 83). Or expressed in another way: the grooves appear mostly to be composed of a number of pieces usually separated by somewhat equal interspaces.

Among the grooves we will consider first the one lettered *ifc* in text-fig. 83. This groove extends from a point somewhat postero-latero-ventrally to the orbital opening forwards as far as the prenasal part of the cephalic shield. On account of its position it is obvious that this groove in its posterior and infraorbital parts must have been innervated by lateralis fibres which as in the Cephalaspids accompanied the n. trigeminus proper and accordingly by the lateralis fibres which formed the homologue of the n. buccalis lateralis of fishes and Petromyzontids, while in its most rostral preorbital part it seems rather likely that it was supplied by lateralis fibres, that were associated with the n. profundes, and thus possibly by lateralis fibres which perhaps formed the equavalent of the n. ophthalmicus lateralis of fishes and Petromyzontids. In virtue of its mode of innervation, therefore, the groove corresponds in the main to the infraorbital groove of the Cephalaspids (cf. text-figs. 76, 77 and pp. 235—239 above) and the infraorbital canal of fishes, but it has in addition a preorbital part which perhaps is homologous with an anterior part of the supraorbital sensory canal of fishes. In the Cepahalaspids in which the sensory canal system is known so far, that anterior part is entirely absent (cf. text-figs. 76, 77). Despite the possibility that the groove of *Tremataspis* under consideration thus perhaps has a supraorbital component, it will for the sake of simplicity be referred to merely as the infraorbital groove.

Posteriorly to the infraorbital groove there follows another longitudinal groove lettered *lc* in text-fig. 83. This latter groove which meets the infraorbital one at a more or less pronounced angle, open towards the lateral side, passes off in a posterior direction dorso-medially to the lateral electric field and probably continued on to the lateral surface of the trunk beyond the cephalic shield. It was certainly innervated by postotic lateralis branches which accompanied the n. glossopharyngeus and the n. vagus during their exit from the cavum



Text-fig. 83. *Trematapsids schmidti.* Cephalic shield. A in ventral and B in dorsal view. After PATTEN 1903, (1903 a).

c, transversal commissure between the anterior ends of the dorsal lateral lines of both sides; *cma*, transversal groove probably corresponding to the middle head-line of pit organs of fishes; *cmm*, transverse groove corresponding either to the posterior head-line of pit organs or to the supratemporal commissure of fishes (not present in all specimens); *dc*, dorsal lateral line; *d. end*, opening for the ductus endolymphaticus; *dsf*, dorsal electric field; $ebr.c_1$, $ebr.c_{10}$, external branchial openings; *f. cn*, circumnasal fossa; *ifc*, infraorbital groove; *lc*, main lateral line; lsf_1, lsf_2, anterior and posterior lateral electric fields; *m*, mouth opening; na_1, na_2, anterior and posterior devisions respectively of the nasal opening (the anterior one really formed the opening of the hypophysial sac); *orb*, orbital opening; *pin*, pineal foramen; *pc*, suprapineal groove.

cerebrale cranii, and because of this and of its position it is certainly the main lateral line.

On the posterior part of the cephalic shield there is, rather close to the median line, a paired rather short longitudinal groove lettered *dc* in text-fig. 83, a groove, which can only be an anterior part of the dorsal lateral line of fishes, Petromyzontids (cf. STENSIÖ 1926, text-fig. 7) and Pteraspids (STENSIÖ 1926). In the Cephalaspids no corresponding groove has been found (cf. text-fig. 76, 77).

Besides the grooves now described, which are all longitudinal or at least chiefly longitudinal, there are four transversal ones, the three most anterior ones of which (*pc*, *cma*, *cmm*) correspond in all respects to the three transversal grooves *pc*, *cmm* and $cmm_1 + cmm_2$ respectively of the Cephalaspids (text-figs. 76, 77). Attention should, however, be called here to the fact that the third of these grooves (*cmm*) counted from in front often seems to be absent. Finally the fourth and most posterior transversal groove (*c*) forms a commissure between the anterior ends of the anterior portions of the dorsal lateral line of both sides and has no homologue in Cephalaspids.

Whether any lateral line grooves were present on the lower side of the cephalic shield and on the plates which closed the oralo-branchial fenestra I have not had the opportunity to investigate myself. According to the restorations published by PATTEN, however, this was not the case.

As is evident from the account just given of it, the sensory canal system of *Tremataspis* is in most respects very similar to that in Cephalaspids, and there can be no doubt that both have been derived from a common ancestral type. As with regard to the transversal commissures it is nearest comparable to that in *Palaeaspis* (cf. STENSIÖ 1926), it seems very likely that it has been derived from a somewhat *Palaeaspis*-like one and that it is to be considered as highly specialized. In this connection it should perhaps also be pointed out that, in the development and position of the infraorbital groove, it shows a certain resemblance to the *Antiarchi*. This resemblance to the *Antiarchi*, however, is certainly a parallelism caused by the shifting of the orbits towards each other on the dorsal side of the head.

The electric fields of *Tremataspis* have already been referred to several times. As is seen from text-fig. 83, they are much less developed than in the *Cephalaspidae* and, contrary to what is the case in these, the lateral one is always subdivided into two separate fields, an anterior (lsf_1) and a posterior one (lsf_2). Otherwise they appear in all respect to have been as in the *Cephalaspidae*. Now since in the *Cephalaspidae* we know their structure rather well it is fully evident that both in these and in *Tremataspis* they must have been either electric organs, as supposed by me in this work, or else sensory organs of a special kind, as suggested by WIMAN (1919, pp. 89—94).

The facts now brought forward concerning its organization show quite distinctly that *Tremataspis* is very closely allied to the *Cephalaspidae* and that it probably has evolved from a Cephalaspid-like ancestor. It differs from the *Cephalaspidae* in the absence of cornua, pectoral sinus and pectoral fins, in the subdivision of the lateral electric field into two, an anterior and a posterior one, and in a somewhat different structure of its exoskeleton. And because of these differences it must be referred — as has been done by all recent palaeoichthyologists — to a family of its own.

After this account on *Tremataspis* a few remarks should also be given on *Didymaspis*. It has already been pointed out above that *Didymaspis* agrees with *Tremataspis* with regard to the extent of the interzonal part, while on the other hand in the presence of small though distinct cornua it approaches the Cephalaspids. Moreover I have been able to observe that with regard to the infraorbital groove it shows rather intermediate conditions between *Tremataspis* and the Cephalspids, and that the external surface of its exoskeleton is ornamented with numerous small tubercles exactly as in many Cephalaspids, while *Tremataspis*, as we know, has the superficial layer of the exoskeleton quite smooth. The development of its electric fields and the minute structure of its exoskeleton are both unknown so far, but it seems not improbable that they will help greatly in elucidating the closer affinities of *Didymaspis*. With our present knowledge of it we can only say that *Didymaspis* in many characters is a transitional form between the two families *Cephalaspidae* and *Tremataspidae*, and that at present it cannot be decided with certainty to which of these two families it really is to be referred.

Now since the families *Cephalaspidae* and *Tremataspidae* undoubtedly are very closely allied, and since in addition, as we shall see, they differ in many respects from other Ostracoderms, it is quite justified to unite them into one group for which I retain the name *Osteostraci* proposed by LANKESTER.

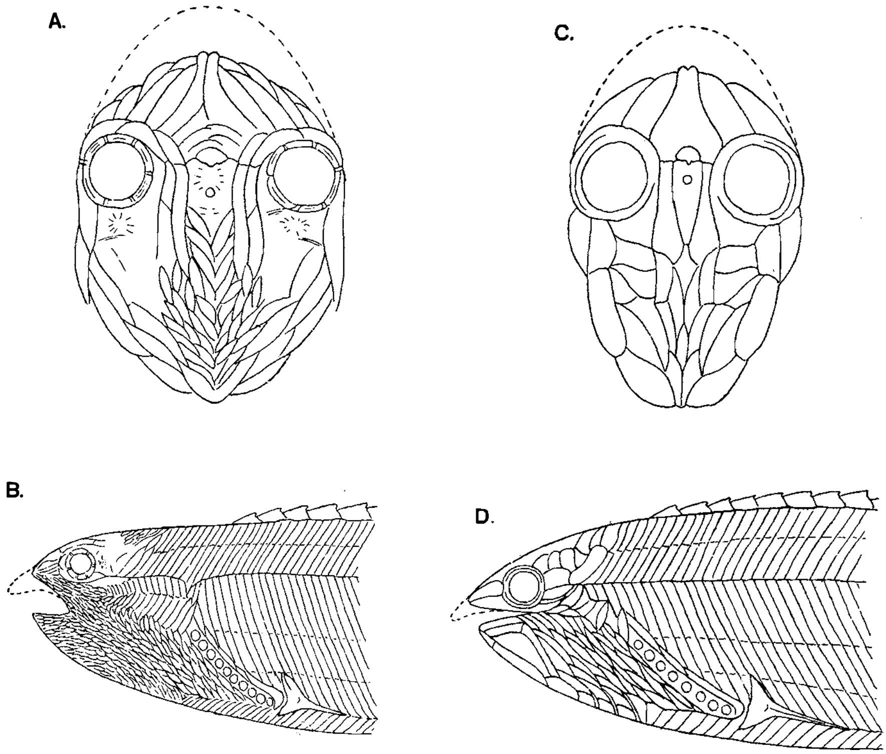
Anaspida.

Through the excellent monograph published by KIAER in 1924 on the *Anaspida* from Norway the range of our knowledge of the group *Anaspida* as a whole has become greatly extended. In fact we have through the said monograph by KIAER obtained a good idea of the exoskeleton and general plan of organisation of the group.

From the account given by KIAER it is easily seen that the orbital entrances, the nasal aperture and the pineal foramen with regard to their mutual positions were very much as in the *Cephalaspidae* (cf. text-fig. 84) — a condition to which attention was called by KIAER himself. And on account of this the conclusion readily suggest itself that the anterior parts of the head with regard to general features were of a similar type as in the *Cephalaspidae*. In this connection it should further be pointed out that, as is distinctly seen in several of the text-figs. given by KIAER (cf. text-fig. 84 in the present work), the unpaired nasal aperture of the Norwegian forms consists of a wide anterior division and a small posterior division, the latter of which forms a notch in the posterior margin of the former. The nasal aperture in the Norwegian forms is thus very suggestive of that in the *Cephalaspidae* with regard not only to the position but also to the shape. And *ex analogia* me may therefore conclude that the anterior wide division was the external opening of the hypophysial sac, while the posterior small division constituted the nasal opening proper. Accordingly the *Anaspida*, like the *Cephalaspidae*, *Tremataspidae* and *Cyclostomata*, had a hypophysial sac but on account of the considerable width of its rostral opening just described it seems very probable that this hypophyseal sac was more strongly developed and wider at least than that in the *Cephalaspidae* and *Tremataspidae.*

As has already been pointed out by KIEAR, the labyrinth cavity must have been situated in the normal way close behind the orbit. And there is no reason to doubt that the otic region was well developed. Concerning the occipital region, on the other hand, KIAER arrives at the conclusion that probably this was entirely lacking, the endocranium, as he expresses it (p. 84), probably having been only a "palaeocranium". The reason advanced by KIEAR for this view is that the exoskeleton of the posterior parts of the dorsal side of the head exhibits a certain metameric disposition, which seems to indicate that myomeres were present almost as far forwards as the orbits, and accordingly that the vertebral elements corresponding to these had retained their independence and not fused with each other and with the endocranium into an occipital region. And it must be admitted that this reason, at least at first, appears to the very plausible. But if we take inte consideration the fact that the head, as KIAER himself called attention to, at least with regard to the disposition of the exoskeleton, is distinctly bounded from the trunk even dorsally, this seems not to be in full harmony with KIAER's opinion. And further if we take into consideration the fact that the otic region, even if it was very strongly developed, cannot have reached as far back as to the boundary between the head and the trunk, there are, in my opinion, also facts which point to an opinion exactly the reverse of that advanced by KIAER. Expressed in another way the reasons brought forward by KIAER for his opinion that the occipitel region was absent are far from decisive, but it is even possible that there was an occipital region. The difference between the *Anaspida* and the *Osteostraci* with regard to the backward extension of the endocranium may therefore perhaps not be so considerable; and it is even not quite imposible that the *Anaspida* might have had an occipital region with a similar backward extension as those forms among the *Cephalaspidae* which have the interzonal part of the cephalic shield short. Perhaps it deserves also to be emphasized here that the number of segments composing the occipital region among the vertebrates is subjected to rather considerable variations (cf. GAUPP 1906, pp. 593—609) and that on account of this, from a morphological point of view, less stress should be laid on the degree of development of the occipital region than has in fact really been done. We shall have the opportunity of discussing this question more in detail below in the account given of the Cyclostomes.

Since the common external opening of the hypophysial sac and the olfactory organ lies exactly as in the *Cephalaspidae*, it is easy to conclude that, as in these and in the Petromyzontids, the preolfactory



Text.-fig. 84. Heads of *Pterolepis* and *Rhyncholepis* in dorsal and lateral views. Chiefly after Kiear in 1924, but slightly modified in the most rostral parts. *A*, *B*, *Pterolepis;* *C*, *D*, *Rhyncholepis.*

part of the head must be formed by the upper lip, and hence that it is of a visceral origin (cf. pp. 121—135 above and the accounts of the *Heterostraci* and *Cyclostomata* below).

That the *Anaspida* and the *Osteostraci* have much in common with regard to the shape and position of the external branchial openings was strongly emphazised by Kiaer; and with our present knowledge of the *Osteostraci* it is still easier for us to see that this was the case. Kiaer also correctly pointed out that the *Anaspida* had lost the homologues of the anterior branchial openings of the *Osteostraci* and that on account of this they were more specialized than the *Osteostraci.*

The mouth of the *Anaspida* in its fossil state of preservation is probably terminal, as was pointed out by Kiaer; but it does not appear to be quite a matter of course that it was so also in the living animals. In order to elucidate this question we shall turn to certain of the figures given by Kiaer, especially to those reproduced in text-fig. 84 in the present work. As we find in those two of these figures (A. C.) which exhibit the exoskeleton of the dorsal side of the head, the most anterior bones which constitute the rostral area, or more correctly the covering of the rostral part of the visceral endoskeleton, do not form a smooth rostral margin, but certain of them project forwards beyond the others etc. In fact the anterior border line of the rostral area of bones is such that we are forced to the conclusion that it did not form the rostral border in the living animals but that anteriorly to it there was uncalicified tissue which was not covered by the exoskeleton. This uncalcified tissue thus formed the real rostrum in the living Anaspids; but it is imposible to decide at present how it was shaped and how far forward it extended, whether it formed only a very narrow zone in front of the rostral area or whether it was longer. But it may be important to call attention to the circumstance that it need not have been very long to have caused the mouth to get a decided ventral position, very much as shown in text-fig. 84 B and D.

The uncalcified rostral part of the head just considered evidently formed at least the dorsal boundary of the mouth. Since as has been pointed out, we know nothing either of the shape or of the extent of this part, it is very difficult to decide whether the mouth, as supposed by KIAER, might have been to a certain extent transformed into a gnathostome direction or whether it was a suctorial mouth.

The anterior part of the visceral endoskeleton that had no gills was probably rather different from the corresponding part in the *Osteostraci* and certainly, as has been pointed out by KIAER, it was more specialized than that; but how it was is difficult to say. That there was a sort of palatoquadrate in a very primitive stage of development as maintained by KIAER is not quite impossible. But if we pay attention to the fact that the mouth lies strikingly far in front of the branchial openings, exactly as it does in the Cyclostomes, it appears, at least to me, more probable that the anterior part of the visceral endoskeleton instead was more or less Cyclostome-like and that the mouth on account of this was a suctorial mouth. Since, however, we lack the necessary suppositions for a definite judgement of these questions, I think we had better leave them undecided for the present.

Concerning the posterior part of the visceral endoskeleton — or, more exactly, the part of the visceral endoskeleton that still had functional gills — already KIAER fully realised (pp. 88, 90) that it could not have consisted of ordinary arches. And that KIAER at that time was able to perceive this is really wonderful. For us it is now easy to conclude that it probably formed a continuous piece of cartilage which was inclined forwards and which corresponded in the main to the postbranchial wall of the *Cephalaspidae*. In addition it is very conceivable that it was continuous with the endocranium antero-dorsally and that the n. vagus left the cavum cerebrale postero-dorsally to its most antero-dorsal part.

All facts known hitherto definitely indicate that *Lasanius*, with regard to the visceral endoskeleton, must have been like the other Anaspids. And accordingly, so far as I can see, everything suggests that KIAER is right when in *Lasanius* he locates the branchial region in front of the bars which earlier had been interpreted as branchial bars and considers these bars as homologues of dermal shoulder girdle-plates of the other Anaspids. The attempt recently made by STROMER to maintain the old interpretation of these bars as branchial bars can thus certainly be ignored (cf. STROMER 1926, pp. 93—95; cf. also KEMNA 1903, p. 381).

The forward inclination of the posterior part of the visceral endoskeleton shows that the posterior part of the branchial region was situated beneath the endocranium, as in the *Cephalaspidae*. In addition the external branchial openings of each side lie in a series which is inclined forwards and thus in much the same way as the posterior branchial openings of the *Cephalaspidae* would do if in the latter the head became reduced in breadth and got a more normal shape. Accordingly there is reason to believe that the *Anaspida* might have evolved from benthonic forms with a somewhat Cephalaspid-like shape and thus that they are secondarily adapted to a nectonic mode of living. In harmony with this is also the circumstance that the mouth, as has been pointed out above, perhaps had a ventral position. I thus arive at an opinion which is widely different from that which seems to be current and according to which the *Anaspida* would be primitive nectonic forms, (WOODWARD, 1920, pp. 27; KIAER 1924, p. 124).

While in the *Cephalaspidae* the exoskeleton of the dorsal and lateral sides of the head forms a continuous piece of bone, the exoskeleton of the corresponding places in the *Anaspida* is, as we know, composed of a great number of small more or less scale-like plates. At present I find it impossible to decide whether in this respect the *Cephalaspidae* are more primitive than the *Anaspida* or the reverse. With regard to the exoskeleton on the ventral side of the head and with regard to the exoskeleton of the trunk, on the contrary, the *Anaspida* and the *Cephalaspidae*, exhibit several striking agreements — a fact which was pointed out already by KIAER.

Since *Lasanius* has typically Anaspid dorsal spines and in addition it seems to have faint traces of a dermal skeleton (cf. KIAER 1924, p. 68), and since it otherwise seems to be rather closely related to the other Anaspids with regard to its general organization, I cannot agree with KIAER when he maintains that the slight development of the exoskeleton in this form is primitive. But, like TRAQUAIR, I take it to be secondary, arisen by reduction (cf. TRAQUAIR 1899 c, p. 858; KEMNA 1903, p. 379). It may further be noted that a hard exoskeleton is found not only in the *Anaspida* but also in all other groups of Ostracoderms, and it seems therefore certain that a hard exoskeleton occurred already in the ancestors of the *Anaspida*. Thus we have in this an additional support for the opinion that the exoskeleton of *Lasanius* is not in a primitive stage but that it must be in a rather advanced stage of reduction.

On the other hand I fully agree with KIAER in his interpretation of the spine-bearing plates and the spines which occur in the Anaspids behind the branchial region. I too consider that these plates cannot be anything else but exoskeletal plates developed in relation to an endoskeleton shoulder-girdle and that the spines on these plates may be either remains of the pectoral fin itself — and this seems most probable — or homologous of the cornua of the *Cephalaspidae*.

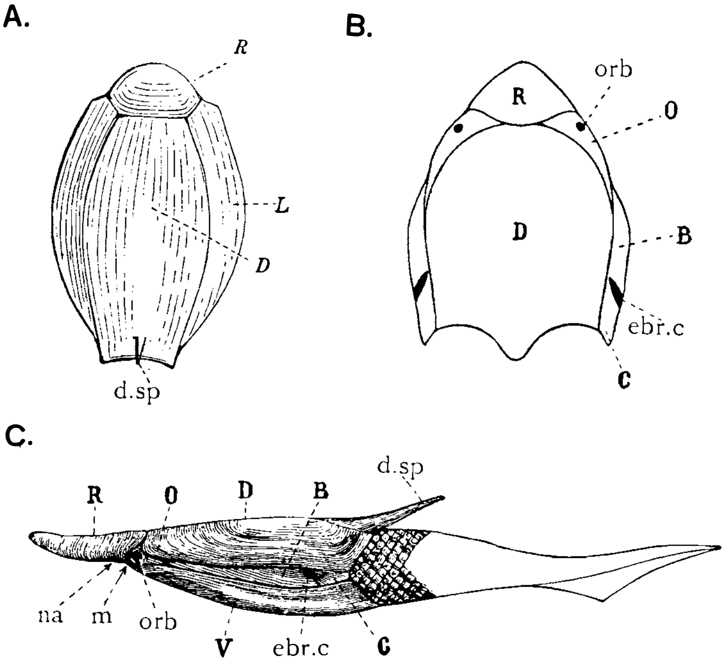
It is of great importance that among the *Anaspida* also we thus have traces of pectoral fins. And since, as we shall see, not only the *Anaspida* and the *Osteostraci* but also at least certain of the *Heterostraci* have similar traces of pectoral fins, we may conclude that the pectoral fins or homologues of these, unless they had arisen independently in different groups — which seems very unlikely — must be very old structures which were present already in the ancestors of the *Osteostraci*, *Anaspida* and *Heterostraci*.

That the *Anaspida* might be allied to the *Cephalaspidae* was already strongly suspected by TRAQUAIR (1899c, pp. 837, 858—859), and that this really is the case was confirmed by KIAER. The researches carried out by me on the *Cephalaspidae* show that, despite the differences between them, the *Anaspida* and the *Osteostraci* are in fact so closely related to each other that it is evident that they must have evolved from common ancestors.

From the account given below we shall find that the *Anaspida* are not anything so closely allied to other Ostracoderms as they are to the *Osteostraci*, and that, on account of this, they must be assigned to the same division of the Ostracoderms as these.

Heterostraci.

The *Heterostraci* are now a days generally subdivided into the families *Coelolepidae*, *Drepanaspidae*, and *Pteraspidae*. In addition by certain writers *Astraspis* and *Psammosteus* have both been separated from the *Drepanaspidae* and made types of separate families, the *Astraspidae* (EASTMAN 1917, pp. 237—239: SCHLOSSER 1923, pp. 31—32) and the *Psammosteidae* (GOODRICH 1909, p. 198; and others) respectively. Finally the family *Gemündinidae*, which was established by TRAQUAIR (1903, p. 734—736) for the very doubtfull vertebrate *Gemündina*, was recently placed to the *Heterostraci* by SCHLOSSER (SCHLOSSER 1923, p. 30). It may be worthy of remark here, however, that at present there are no facts known which justify the establishment of new families either for *Psammosteus* or for *Astraspis*, but both these genera may very



Text-fig. 85. A, *Cyathaspis banksii*, dorsal shield. After LANKESTER 1868. B, *Pteraspis gosseletti*, dorsal shield. After LERICHE 1906. C, *Pteraspis rostrata* carapace and anterior part of trunk in lateral view. After WOODWARD 1891 (1891 a), slightly altered. *B*, branchial plate; *C*, cornual plate; *D*, dorsal median plate; *L*, dorso-lateral plate; *O*, orbital plate; *R*, rostral plate; *V*, ventral shield; *d.sp*, dorsal spine; *ebr. c.* external branchial opening; *m*, mouth; *na*, nasal opening; *orb*, orbital opening.

well be assigned to the family *Drepanaspidae.* And as to the family *Gemündinidae*, it is so imperfectly known that it cannot be decided whether it really has anything to do with the *Heterostraci* or not.

Under such conditions I can confine myself here to deal only with the families *Coelolepidae*, *Drepanaspidae* and *Pteraspidae*; and a among these we shall first consider the *Pteraspidae*, which are the best known, then the *Drepanaspidae* and lastly the *Coelolepidae.*

Family Pteraspidae.

The representatives of this family have, as we know, the head and an adjacent anterior part of the trunk provided with a strong carapace. This carapace consists of a dorsal shield and a ventral shield, the former of which always projects forwards beyond the latter and is so developed anteriorly that with its anterior part it surrounds the rostrum not only dorsally and laterally but also ventrally. Between the ventral portion of the rostral part of the dorsal shield and the anterior edge of the ventral shield there is always in the fossil state of preservation a considerable gap, a gap which, as we know, must have been to a great extent occupied by the mouth, which thus had a ventral position, as in the *Cephalaspidae.*

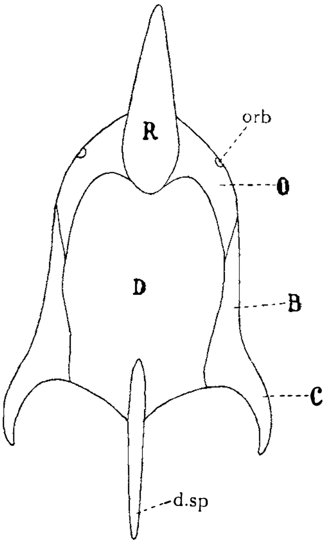
The ventral shield is, as far as known, always a single piece. The dorsal shield may be a single piese too, as in *Palaeaspis* and perhaps also in *Tolypaspis*, but often it is composed of a several plates. Thus in *Cyathaspis* (text-fig. 85 A) it seems, at least in certain cases, to consist of two unpaired median plates — the rostral plate (*R*) and the dorsal median plate (*D*) — and one paired plate along each side — the so-called cornutal plate, or, as it will be called here, the dorso-lateral plate (*L*). And in the Devonian *Pteraspis*-species (text-fig. 85 B, C; 86) it is always made up of a similar number of unpaired plates and at least of one more paired plate, the dorso-lateral plate having in them divided into an orbital plate (*O*) surrounding the orbital entrance, and a posterior plate (*B*, *C*), which we may call the branchio-cornual plate. According to observations made by myself the branchio-cornual plate, as thus defined, seems at least in certain of the Devonian *Pteraspis*-species (text-fig. 85 C) to be subdivided in its turn into an anterior plate, which we shall call the branchial plate (*B*), and a posterior plate, to which the term of cornual plate (*C*) will be applied.

Palaeaspis, Tolypaspis, and *Cyathaspis* all being mainly or entirely Silurian forms, we find from what has been set forth that the dorsal shield of the earliest known Pteraspids was less subdivided into plates than in the Devonian *Pteraspis*, a fact which is of much interest and which we shall discuss further in another connection below.

As we know, there are in *Palaeaspis* and *Cyathaspis* on the lower side of the dorsal shield impressions of several internal structures (text-fig. 87). And now since we know well the organization of the *Osteostraci*, this enables us to understand better than before by which organs these impressions were caused. Thus there can be no longer be doubted that the paired >-shaped groove (*c. sem. ant*, *c. sem. post,* text-fig. 87) is really what it has long been suspected to be, viz. an impression of the anterior and posterior semicircular canals. It is also evident that the pit (*pin*, text-fig. 87) which has been interpreted as the pineal pit really lodged the pineal organ. Further it is not difficult to see that the markings which have been considered either as impressions of gill-arches or of Cyclostome like gill-sacs (*k*, text-fig. 87; both the lateral angular and the medial straight markings) must in fact have been caused by gills of a similar type as in the *Cephalaspidae.* Moreover, as has been earlier pointed out by myself (STENSIÖ 1926, p. 10), there is in certain Silurian forms a median longitudinal groove-like impression (*cv*, text-fig. 87), which from a point somewhat behind the pineal pit extends rather far backward. And, as I have also pointed out, this longitudinal groove-like impression must probably have been caused by the brain or more correctly by the most posterior part of the endocranium enclosing the medulla and not, as recently maintained by JAEKEL (1926, pp. 177—179), by a gland or an organ regulating the temperature of the brain. Finally the paired shallow but rather wide fossa (*olf*, text-fig. 87) in *Cyathaspis integer*, that JAEKEL (1926, p. 178) assumes to have formed part of the roof of the olfactory organ, must certainly have been caused by that organ, since this must have been situated far forwards just anteriorly to the mouth and so that it had its external opening on the ventral side of the rostrum.

In this connection it should also be pointed out that the openings in *Pteraspis* which have been held to be orbital openings, really must be so. And it is also clear that the correspondingly situated notch (*orb*, text-fig. 87) in the ventral margin of the dorsal shield of *Palaeaspis* and *Cyathaspis* must have formed the dorsal boundary of the orbital opening.

While thus in *Palaeaspis* and *Cyathaspis* the lower side of the dorsal shield has several more or less distinct impressions of internal organs we find in the Devonian *Pteraspis*-species hardly anything more of such impression than the pineal pit, which, however, as a rule, is very distinct. That this is the case is highly interesting, since it seems to suggest that the carapace in the oldest appearing *Pteraspidae* reached deeper inwards than in the later ones. Or, expressed in another way, the facts known so far seem to indicato that the carapace of the Silurian *Pteraspidae* was relatively thicker than that of the Devonian *Pteraspidae*, and that this condition was due to the fact that in the former it was more strongly developed basally than in the latter. There would thus be certain facts which would indicate that the *Pteraspidae* from their appearence in the Silurian until they became extinct towards the middle or end of the Devonian degenerated with regard to the hard skeleton; and in full harmony with this is also the fact to which attention has already been called above, that the dorsal shield of the Silurian *Pteraspidae* is less subdivided into plates than that in the majority of Devonian *Pteraspidae*.



Text-fig. 86. *Pteraspis crouchi.* Dorsal shield. After LERICHE 1924. For explanation of letters see text-fig. 85.

As was pointed out long ago by HUXLEY (1858a pp. 274—278; cf. also LANKESTER 1868, pp. 11—12; ROHON 1893, pp. 78, 79, 83—88, 91—92; LINDSTRÖM 1895, pp. 6—9; DREVERMANN 1904, pp. 285—288; PATTEN 1912, pp. 293—295; etc.) the carapace of the *Pteraspidae* may be considered to be composed of four layers, which we shall here call the basal layer, the cancellous layer, the reticular layer and the superficial layer.

The basal layer (text-fig. 88) varies rather much in thickness in different forms and at different places of the carapace. It consists of thin laminae which are often very distinct. Like HUXLEY and GEBHARDT (1907) I have tried to study these lamellae in detail, but since the material of Pteraspids at my disposal was very badly preserved with regard to minute structure it has been impossible to make out any new details of importance. In one case, however, I was able to see a delicate striation, showing that the lamellae must quite certainly have contained numerous fibres. But whether the fibres in two neighbouring laminae had such a disposition that they crossed each other almost at right angles, as they do in the *Tremataspidae*, or wheter they had another disposition cannot be ascertained. In this connection it deserves to be mentioned that already HUXLEY observed the fibrous structure of the lamellae (1858, p. 275; cf. also GEBHARDT 1907, pp. 74—75). In the material studied by me there was no evidence of any cell-spaces, and despite the statements to the contrary by DREVERMANN (1904, p. 286), GEBHARDT (1907, pp. 74—75) and PATTEN (1912, pp. 293—294), I am inclined to believe that all Pteraspids lacked cell-spaces. In any case the figures given by both DREVERMANN and PATTEN cannot convince me that the structures referred to by these two writers as cell-spaces really are so.

The basal layer is perforated by a number of rather fine canals which not rarely have a winding course. These canals, which traverse the basal layer more or less prependicularly and go to the cancellous layer, evidently transmitted vessels and nerves.

The cancellous layer is so well described by earlier writers that I have nothing to add here concerning it except that the walls of the cancellae are formed by a laminated tissue which lacks cellspaces and which much resembles the tissue in the basal layer. The cancellae certainly lodged vascular sinus which were in communication with each other by means of fine anastomoses which perforated the walls of the cancellae. From the vascular sinus of each cancella there usually issued a few vessels outwards to the reticular layer.

The reticular layer is sometimes rather thin and may in certain forms[1] even be almost lacking, having been replaced by the cancellous layer. It is characterized by its canals, which anastomose with each other abundantly and which basally, towards the cancellous layer, are wider than more superficially and in addition often rather parallel with

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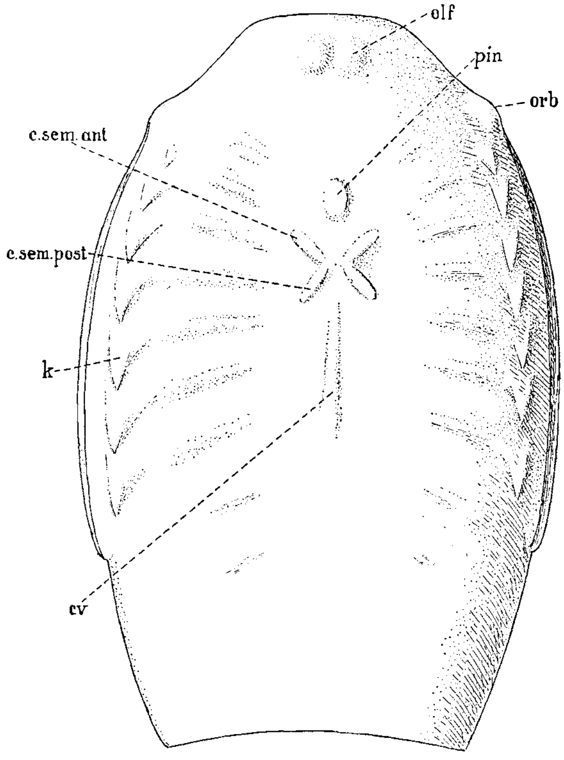
[1] *Tolypaspis* and probably in *Palaeaspis*.



Text-fig. 87. *Cyathaspis integer* KUNTH. Internal surface of the dorsal shield. After JAEKEL 1926. *c. sem. ant*, *c. sem. post*, impressions of the anterior and posterior semicircular canals respectively; *cv*, impression of the part of the endocranium that lodged the medulla; *k*, impression of the gill apparatus; *olf*, impression of the olfactory organs; *orb*, orbital notch; *pin*, impression of the pineal organ.

the surface of the shields. The hard tissue of this layer is more or less distinctly laminated and without cell-spaces.

The canals of the reticular layer chiefly lodged vessels, which, as has been pointed out, ascended from the vascular sinus situated in the cancellous layer. The reticular layer thus lodged a more or less complicated vascular plexus which was situated exactly as the subepidermal vascular plexus of the *Cephalaspidae*. But comparison with the *Drepanaspidae* — in which, as we know (cf. KIAER 1915, pp. 21—38), the reticular layer is very thick and reaches down to the basal layer — show that the vascular sinus of the cancellous layer also pertained to the subepidermal vascular plexus and must be regarded as a specialized basal part of it. The subepidermal vascular plexus of the *Pteraspidae* thus consisted of a deep portion of relatively big vascular sinus which anastomosed with each other, and of a superficial portion of rather fine abundantly branching vessels. And to a certain extent we had thus here a parallel to the conditions in *Tremataspis* (cf. pp. 38—40 above).

Weare thus led to the conclusion that the cancellous layer and the reticular layer together correspond to the middle layer of the *Cephalaspidae*. And, this being the case, it is obvious that the basal layer too is homologous in the *Pteraspidae* and the *Cephalaspidae*. Accordingly the canals which traverse the basal layer of the *Pteraspidae* must correspond to the ascending canals of the basal layer of the exoskeleton in the *Cephalaspidae*, and the subaponeurotic vascular plexus of the

Pteraspidae, if there was one, must thus evidently have been situated basally to the basal layer.[1]

Finally the superficial layer of the carapace of the *Pteraspidae* is very well known through the description by earlier writers. Here, therefore, I have only to emphasise the fact that it is very suggestive of that in certain Cephalaspids. That this is the case can easily be seen from the specimen of *Cephalaspis hoeli* figured in pl. 67, fig. 2 in the present work.

From this review we thus find that the *Pteraspidae* with regard to the minute structure of their shields differ from the *Cephalaspidae* chiefly only in two respects: in a somewhat different development of the middle layer and in the absence of cell-spaces in the middle and basal layers.

As we have found, the strange development of the middle layer in the *Pteraspidae* is probably to be considered as a specialization arisen from conditions rather similar to those in the *Cephalaspidae*; and it thus follows that presumably the difference in this respect between the *Pteraspidae* and the *Cephalaspidae* is of a rather slight importance from a morphological point of view.

The question wheter the absence of cell-spaces in the shields of the *Pteraspidae* is a primitive or a secondary feature has not been discussed in a satisfactory way be earlier writers; and we shall therefore have to deal with it here. As we have seen, the basal layer and the middle layer (middle layer = cancellous + reticular layers of HUXLEY'S description) are distinctly laminated, and, as we have also seen, a fibrous structure can be traced at least in the basal layer. These facts combined with the circumstance that the exoskeleton beyond question was situated in and occupied the entire thickness of the corium show that the middle and basal layers simply represent the corium aponeurosis in a rather unchanged condition. And as this is so, we are forced to the conclusion that the basal and middle layers arose ontogenetically in the same way as the corium aponeurosis of recent craniate vertebrates, and that because of this they must during the ontogenesis have contained cells between the various lamellae.

Since most palaeontologists are probably unaware how a corium aponeurosis of the type here in question develops ontogenetically, it will be useful to give a brief account of this here, and in doing so I shall

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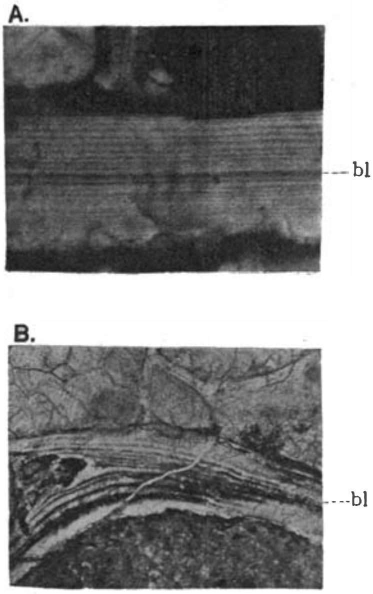
[1] The opinion at which I have arrived here concerning the function of the cancellae and the different canals in the shields of the *Pteraspidae* is thus very different from that advanced by GEBARDT (1907, pp. 72—79). It may be added here that my opinion in this case is based not only on my observations in the *Cephalaspidae* but also on the conditions in the recent Cyclostomes in which both a subaponeurotic and a subepidermal vascular plexus are present (cf. the account on the Cyclostomes below).

chiefly follow E. HOLMGREN (1920, pp. 152—153). The development begins in the way that certain connective tissue cells, which are termed fibroblasts, arrange themselves into a single almost epithelium-like stratum immediately beneath the basal surface of the epidermis and give rise to a layer with collagene fibres between themselves and the epidermis. The collagene fibres in this stratum are parallel with each other and with the basal surface of the overlying epidermis. In *Amphioxus* this stage remains as a definite one. In the cranite vertebrates, on the other hand, a new stratum of fibroblasts is soon formed beneath the first, and this second stratum of fibroblasts produces between itself and the first stratum of fibroblasts a second layer of collagene fibres. These fibres are also parallel with each other and with the basal surface of the epidermis, but they cross the fibres in the layer above that was first formed almost at right angles. To the second layer with collagene fibres are soon added still more layers in a similar way as in the case of the first and second ones, and the aponeurosis thus grow in an inward direction by the apposition of new layers basally. Since the collagene fibres in two neighbouring layers are always arranged in such directions that they cross each other almost at right angles the whole aponeurosis gets a distinctly laminated appearance. Most important for us here is to notice that each of the fibroblast strata lies just beneath the layer or lamella of collagene fibres formed by it and that thus the fibroblasts are enclosed into the aponeurosis formed by them.



Text-fig. 88. Basal layer of the exoskeleton of two Pteraspids, showing the lamination. A, of *Palaeaspis*?; B, of *Pteraspis*.

The conditions in recent craniate vertebrates thus show that a corium aponeurosis like that in the basal and middle layers of the carapace of the *Pteraspidae* cannot be imagined to have developed ontogentically without cells becoming enclosed in it between its various lamellae. And we are thus forced to assume that cells originally must have formed the basal and middle layers of the carapace of the *Pteraspidae* and have been enclosed between the lamellae of these layers, though they became reduced already in very young larvae. Accordingly everything seems to indicate that the absence of cell-spaces in the shields of the adult *Pteraspidae* is a secondary feature, and thus that the *Pteraspidae* in this respect are more specialized than the *Osteostraci*. Further it is clear that, if the ontogenetical development of it was as

I home assumed here, the hard tissue that constitutes the middle and basal layers of the carapace of the *Pteraspidae* is in fact true bone.

Summarizing the results of this breaf analysis, we find that both the chief characters in which the *Pteraspidae* differ from the *Cephalaspidae* with regard to the microscopic structure of the exoskeleton are secondary, arisen by specialization. It is therefore fully evident that both these characters are of slight importance from a morphological point of view. And as far as can be judged at present, there is even reason to believe that the *Pteraspidae* arose from forms which, so far as the minute structure of the exoskeleton is concerned, were rather suggestive of the primitive *Cephalaspidae.*

Before leaving the microscopic structure of the carapace of the *Pteraspidae* we should do well to notice that the basal layer, just as in the *Cephalaspidae*, may have consisted at least most basally of lamellae formed by the perichondrium of the endoskeleton and accordingly that it probably was not of a pure dermal origin. A strong support for this opinion is furnished by the presence of the impressions of internal structures on the lower side of the dorsal shield. Several of these impressions would be difficult to explain unless the dorsal shield had been very intimately connected with the endoskeleton beneath it.

No traces of structures corresponding to the mucous canals of the *Tremataspidae* or of the interareal grooves of the *Cephalaspidae* are known in the *Pteraspidae* unless these structures are represented by the longitudinal grooves or canals which always occur between the ridges of the superficial layer of the *Pteraspidae.*

Turning next to the endoskeleton of the *Pteraspidae* that was enclosed in the carapace, it is quite obvious that this as a whole must have consisted of an uncalcified rather solid tissue, certainly some sort of cartilage. Since it is difficult to imagine that ossification of the endoskeleton took place quite independently in the Ostracoderms on the one hand and in the other craniate vertebrates on the other, it seems at present most likely that a more or less ossified endoskeleton was present already in the common ancestors of Ostracoderms and other craniate vertebrates. And under such circumstances it seems most probable that the absence of bone in the endoskeleton of the *Pteraspidae* is a secondary character due to reduction.

The development of the carapace of the Pteraspids and the knowledge which we now posess of the endoskeleton of the *Osteostraci* makes it impossible to imagine that the endoskeleton of the Pteraspids that was surrounded by the carapace could have been subdivided into numerous independent elements, as in fishes and higher vertebrates, but that as a whole it must have been mainly a continuous structure somewhat as in the *Osteostraci.* From facts to be advanced below it is obvious that, exactly as in the *Osteostraci*, it consisted not only of the endocranium and the visceral endoskeleton but also of the endoskeletal shoulder-girdle.

As far as can be judged from the impressions of the internal structures on the lower side of the dorsal shield and from the position of the olfactory organ, the endocranium must have been long and — contrary to what is the case in the *Cephalaspidae* — strikingly broad anteriorly. Since there can have been only very slight mobility in the most anterior part of the trunk enclosed in the carapace it seems already from this highly probable that the most anterior vertebral elements had fused with each other and with the endocranium and formed a long occipital region; and when, as we have seen, we find an impression of a postotic endocranial part far back on the ventral side of the dorsal shield (text-fig. 87), it cannot be doubted that there was an occipital region and that this was long, probably even longer than in most of the *Cephalaspidae* with a long interzonal part in the cephalic shield. The otic region was probably rather short and not so very much wider than the occipital region. It enclosed a well developed labyrinth which certainly in its chief characters recalled that in the *Cephalaspidae*. The orbitotemporal region was probably broad, but short in proportion to its breadth, a condition which was due the position of the orbits far apart from each other on the lateral sides of the head. The eyes were certainly small. The ethmoidal region was also broad and was so situated that it formed the rostrum, while in the *Cephalaspidae*, as we have seen, the rostrum was formed by an anterior part of the visceral skeleton. We thus have here an important difference between the *Pteraspidae* and the *Cephalaspidae*, and it is highly interesting to find that in this respect the *Pteraspidae* agree with *Myxine*, whereas the *Cephalaspidae* are like *Petromyzon*. The olfactory organ of the Pteraspids, which, as has already been pointed out, was situated so that it opened outwards on the ventral side of the rostrum close in front of the mouth, also obviously had a position similar to that which it has in *Myxine*, while that of the *Cephalaspidae* lies as in *Petromyzon*. Now since the olfactory organ as well as the hypophyseal sac, in *Petromyzon* arises ontogentically on the ventral side of the head close in front of the mouth and accordingly in early embryonic stages has a similar position as in the *Pteraspidae* and *Myxine*, it seems certain that in the *Osteostraci* and *Anaspida* also it must have arisen on the ventral side of the head close in front of the mouth opening. Accordingly we find that the *Pteraspidae* with regard to the position of the nasal aperture probably like the Myxinoids had retained more primitive conditions than the *Petromyzontidae*, the *Osteostraci* and the *Anaspida*. Attention may further be called to the fact that the olfactory organ of the *Pteraspidae* probably was more distinctly paired than that of the recent *Cyclostomata* and that of the *Osteostraci* and that of the *Anaspida*, and that it perhaps opened outwards with a paired opening. On the other hand, at least as far as can be judged from the conditions in *Cyathaspis integer* (text-fig. 87), it is highly probable that its two halves were situated very close to each other and to the median line, so close even that it may give rise to the question whether they were not partly fused into a single space.

In order to eluctidate more in detail what has just been set forth concerning the differences in the rostral parts of the head in the *Pteraspidae* and *Myxinoidea*, on the one hand, and in the *Osteostraci*, *Anaspida*, and *Petromyzontidae*, on the other, the reader is referred to text-fig. 89, which shows four stages in the development of the anterior portions of the head in *Petromyzon*. As we see in text-fig. 89 A the anterior part of the head in young larvae is very much curved downwards and on the ventral side of it we find most anteriorly the olfactory organ (*n*) and the hypophysial sac (*h*) opening outwards into a common pit. Close behind this pit and separated from it by the upper lip (*u*) follows the stomodaeum. The olfactory organ thus has in this stage a similar position as in the *Pteraspidae*, and it is evident that the anterior end of the head is formed, like that of the *Pteraspidae*, by the postnasal part of the ethmoidal region and thus by the endocranium itself. In the following stage (text-fig. 89 B) the downward curvature of the anterior part of the head is less than in the first one and the common external opening of the olfactory organ and hypophysial sac occupies a more anterior direction. The upper lip is considerably larger than in the former stage. In the third stage (text-fig. 89 C) the downward curvature of the anterior part of the head is only very slightly pronounced. The common opening of the olfactary organ and the hypophysial sac faces antero-dorsally and the upper lip, which is still larger than in the preceding stage, now forms the tip of the head, so that in fact we have here in this respect conditions approaching those in the *Osteostraci* and *Anaspida*. Finally in the fourth stage (text-fig. 89 D) we find the common opening of the olfactory organ and hypophysial sac situated exactly as in the *Osteostraci* and *Anaspida*, and it is also quite clear that the upper lip, now highly enlarged, must correspond to the prenasal part of the head of the *Osteostraci* and *Anaspida* and that the skeletal parts forming the rostrum in these two groups therefore must be of a visceral origin, while that is not the case in the *Pteraspidae* and *Myxine*[1]. We thus find here that with regard to the origin and homologues of the rostrum the *Pteraspidae* and the *Myxinoids*, on the one hand, and the *Osteostraci*, the *Anaspida* and the *Pteromyzontids* on the other hand, agree with each other. It is also obvious that in the

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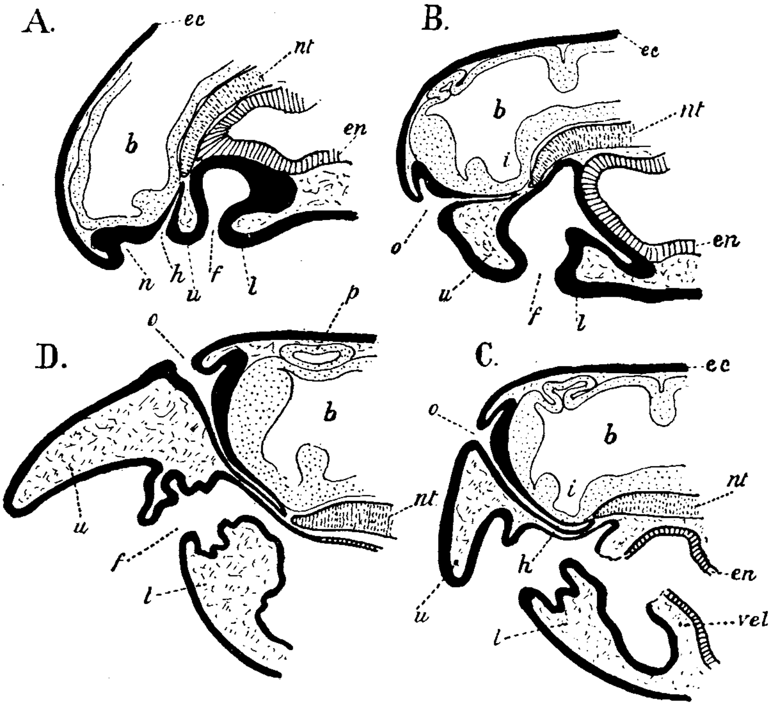
[1] In certain fishes, such as Elasmobranchs and sturgeons, the tip of the rostrum is also formed by the ethmoidal region.



Text-fig. 89. *Petromyzon.* Four stages in the development of the anterior part of the head. Four median longitudinal sections from GOODRICH 1909, after DOHRN. A, the youngest, D, the oldest stage.

b, brain; *ec*, ectoderm; *en*, entoderm; *f*, stomodaeum; *h*, hypophyseal sac; *i*, infundibulum; *l*, lower lip; *n*, olfactory organ; *nt*, notochord; *o*, common external opening of the olfactory organ and hypophyseal sac; *p*, pineal organ; *u*, upper lip; *vel*, velum.

case of the rostrum and the position of the nostril the *Pteraspidae* and *Myxine* must be more primitive than the *Osteostraci*, the *Anaspida* and the *Petromyzontidae.*

As far as can be judged from the impressions on the ventral side of the dorsal shield, the visceral endoskeleton was, at least in its gill-bearing part, much as in the *Osteostraci.* The gills were certainly of entodermal origin, as in the the *Osteostraci* and Cyclostomes, and it is also clear that they must have been more or less sac-like, and on account of this we shall refer to them as gill-sacs. The number of gill-sacs which have left impressions after them in the fossils is about 7, but the total number of gill-sacs was probably still greater, since we must assume that probably the smallest ones most anteriorly and posteriorly did not cause any impressions on the dorsal shield because of the fact that they must have been situated too deeply below this. The most anterior gill-sac which has caused an impression was situated below or slightly in front of the orbit.

Since, as was pointed out by JAEKEL (1911, p. 31, fig. 18) and other writers after him, it is probable that the mouth of the *Pteraspidae* was a suctorial mouth, it seems very likely that certain of the most anterior parts of the visceral endoskeletal had been more or less modified in a Cyclostome-like way.

The gill-sacs did not open outwards independently of each other but the ducts leading outwards from them united backwards into a common external aperture about in the same way as in *Myxine*. Despite the statements to the contrary by certain writers (ABEL 1919, p. 84) this aperture must have been situated on the lateral side of the carapace and not behind this. In *Palaeaspis* and *Cyathaspis* it has not, as far as I know, been observed but it is highly probable that in them it lay in the soft tissue between the posterior parts of the dorsal and ventral shields. In *Pteraspis*, on the contrary, it is often distinctly seen and, as is well known, it lies in the posterior part of the branchio-cornual plate or, when that is subdivided between, the branchial plate and the cornual plate. We thus find here that with regard to the mode of opening outwards of the gill-sacs the *Pteraspidae* presented a striking agreement to *Myxine*[1]. As regards the position of the gill-sacs, on the other hand, it is quite evident that the *Pteraspidae* differed from *Myxine* and other Myxinoids for in the *Pteraspidae* the first gill-sac lay already close behind the mouth while in the Myxinoids the first functional gill-sac is always situated strikingly far behind the mouth. Since, however, there are certain facts which indicate that the gill-sacs in the Myxinoids originally occupied a more anterior position but shifted backwards in connection with the strong development of the rasping tongue, it seems not impossible that at least the anterior gill-sacs of the Myxinoids corresponded to the posterior gill-sacs in the *Pteraspidae* and in the *Osteostraci*.

From the facts known so far concerning the extension of the gill-region backwards it is easy to understand that the most postero-lateral portion of the part of the trunk in the *Pteraspidae* that is surrounded by the carapace corresponds to the endoskeletal shoulder-girdle of the *Osteostraci* and *Anaspida*. It is therefore of much interest to notice that in one of the Downtonian Pteraspid forms from Spitsbergen — a form which was kindly sent to me by KIAER and which will be later on described by him — the cornual plate was developed into a very strong laterally and somewhat posteriorly projecting spine, which obviously corresponds to the cornu of the *Cephalaspidae*. A similarly situated, though much less strongly developed, spine occurs also in *Pteraspis crouchi* (text-fig.

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[1] It must be remembered, however, in this connection that in *Bdellostoma* the gill-sacs opened directly outward independently of each other as in *Pteromyzon*, and that with regard to the mode of opening of the gill sacs outwards *Paramyxine* represents an intermediary stage between *Bdellostoma* and *Myxine*.

86; cf. LERICHE 1924). The presence of this spine is of much interest, as it seems to indicate that primarily there might have been a pectoral fin behind it. And since, as we have seen, a more or less complete pectoral fin occurs in the *Osteostraci* and probably also in the *Anaspida*, it seems very likely that such a fin is a very old structure which was present already in the primitive ancestors of the Ostracoderms and that from them it was inherited by the *Osteostraci* and *Anaspida* as well as by the *Pteraspidae* and their allies.

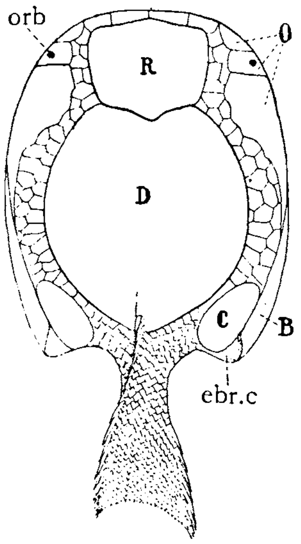
The sensory canal system consists of closed canals in the carapace and, as has been shown by the present author in a previous work (STENSIÖ 1926), it differs much in its disposition from that in fishes, whereas in this respect it presents striking agreements to that in *Petromyzon*. And as was pointed out in the work just quoted these agreements with *Petromyzon* are even so important that they by themselves enable us to conclude that the *Pteraspidae* among recent forms must be nearest akin to the Cyclostomes. It is also obvious that the sensory canal system of the *Pteraspidae* agrees in certain respects with that of the *Osteostraci*, but that as a whole, at least with regard to its disposition, it must be more primitive than the latter, which certainly has been much modified by the displacement of the eyes in a dorso-medial direction and by the development of the electric fields.

From the brief review now given of their organization it is evident that the *Pteraspidae* cannot be allied to the *Elasmobrachii*, as maintained by TRAQUAIR (1899 c, pp. 856—857) and KIAER (1924, pp. 122—123, 129), but that they must be in a similarly low stage of organization as the *Osteostraci*, *Anaspida* and *Cyclostomata* and that they must be assigned to the same branch of the vertebrate stem as these. In a few characters — as, for instance, the microscopic structure of their exoskeleton and the usually complete reduction of the pectoral fins — they are more specialized than the *Osteostraci*. In other characters, on the contrary — such as the construction of the rostrum, the position of the eyes and nasal aperture, the paired appearance of the olfactory organ and the disposition of the sensory canals — they are more primitive than the *Osteostraci*. And accordingly as they differ from the *Osteostraci* in so many important features they cannot be assigned to the same group of the Ostracoderms as these, but they must be placed in a group of their own, a group for which the term *Heterostraci* introduced by LANKESTER in 1870 may be retained.

Family Drepanaspidae.

We first deal with the best known representative of this family *Drepanaspis gemündenensis*.

As we know, *Drepanaspis gemündenensis* is a benthonic form which has the head and an adjacent considerable part of the body broad and



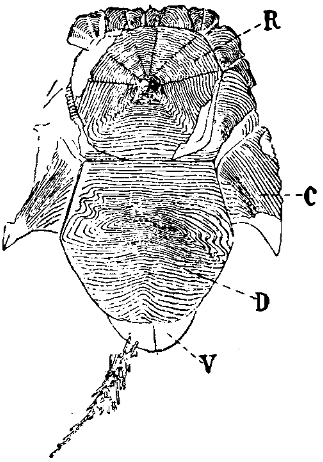
Text-fig. 90. *Drepanaspis gemündenensis.* Dorsal aspect. After Woodward 1920.

B, branchial plate; *C*, cornual plate; *D*, median dorsal plate; *O*, orbital plates; *R*, rostral plate; *ebr. c*, external branchial opening; *orb*, orbital opening.

much depressed in a dorso-ventral direction. The microscopic structure of its exoskeleton, as is shown by Kiaer (1915, pp. 29—38), is as in the *Pteraspidae* — with the exception, however, that the basal part of the middle layer has no such big vascular sinus. As has been pointed out by Dean (1904, p. 64), Kiaer (1919, pp. 29—38) and Woodward (1920, p. 31), Traquair, who first gave a detailed description of the animal (1899 c, pp. 844—847; 1904, pp. 725—731), reversed the dorsal and ventral sides; and it was therefore at first difficult to compare the arrangement of the plates on the anterior widened part with the plates forming the carapace in the *Pteraspidae.* Now, however, it is easily seen that the larger plates (text-fig. 90) are to a certain extent comparable to the plates of the carapace especially in the Devonian *Pteraspis*-species. We thus have plates which at least in the main correspond to the rostral and median dorsal plates, to the ventral shield and to the orbital, branchial and cornual plates of the Devonian *Pteraspis*-species. The orbital plate, however, is subdivided into three smaller ones. And the orbital, branchial and cornual plates do not meet either the ventral plate or the rostral and median dorsal plates, but are separated from these by polygonal small plates. Similar small plates seem also to be present most rostrally along the rostral margin of the rostral plate and in front of the ventral plate. How the majority of these different plates are situated is shown more in detail by text-fig. 90.

Drepanaspis is thus provided with a carapace which in several respects resembles that in the *Pteraspidae*, but which consists of a much greater number of plates than that. Since *Drepanaspis* is from the lower Devonian it seems hardly probable that the strong subdivision of its carapace is primitive, but it is instead more likely that it is secondary, arisen from more typically *Pteraspis*-like conditions.

Since we now know with certainty which is the ventral and which is the dorsal side of *Drepanaspis*, it is easy to understand that, contrary to Traquair's statements (1904, p. 727), the mouth was not terminal but ventral, as in the *Pteraspidae* and that the nasal aperture or apertures must also have had a similar position as in the *Pteraspidae.* It is also evident that the small openings (*orb*, text-fig. 90) which Traquair (1904,



Text-fig. 91. *Phyllolepis concentrica.* Dorsal aspect. After Woodward 1920.

C, cornual plate, developed as a cornu; *D*, median dorsal plate; *R*, rostral plate; *V*, ventral plate (perhaps paired).

pp. 729—730) considered to have been developed for a sensory organ of some sort must be the orbital openings and that the eyes thus were very small. Finally, as pointed out by Woodward (1920, p. 30) there is found an opening (*ebr. c*, text-fig. 90) between the branchial and the cornual plates, if we use the terms for these plates introduced above by me. As far as can be judged, this opening, as suggested by Woodward, must be the external branchial opening. And thus there was also a single external branchial opening on each side just as in the *Pteraspidae.*

The endoskeleton of *Drepanaspis* is not known, and it is therefore likely that it was at least in the main unossified. To judge from the position of the orbits and the mouth, the endocranium was very similar in shape to that of the *Pteraspidae*, and the rostral end of the head was, just as in these, formed by the ethmoidal region. The branchial endoskeleton, the gill-sacs and their mode of opening outwards were also quite certainly of a Pteraspid-type.

The cloacal opening has not been observed but it is very likely that it was situated just behind the ventral plate and thus approximately in the same transversal plane as the external branchial openings. In any case it is obvious that it cannot have been situated much farther backwards, and we thus see that the carapace of *Drepanaspis* in its posterior-median part must enclose the entire body, except the caudal region. It is out of question that the branchial region reached to or almost to the posterior end of the carapace for in such a case there would have been no space left for the viscera. Since even in the earliest appearing *Pteraspidae* only a comparatively short part of the trunk was surrounded by the carapace, we are lead to the conclusion that the conditions in *Drepanaspis* with regard to the strong backward development of the carapace and the position of the viscera in that are secondary.

The position of the external branchial opening suggests that the part of the trunk homologous to the shoulder-girdle was situated postero-medially to the postero-lateral corner of the carapace and that this part was covered dorsally by the cornual plate (*C*, text-fig. 90). Pectoral fins are entirely lacking and, as far as can be gathered, they must have become reduced.

What has now been set forth concerning the position of the shoulder-girdle renders it at once obvious that the lateral much flattened parts of the carapace cannot be considered either as pectoral fins or as homologues of the cornua of the ***Cephalaspidae*** and ***Pteraspidae*** (cf. TRAQUAIR 1899 c, p. 846—847; HOWES 1900, p. 309; KEMNA 1903, pp. 373—375).

The caudal fin was probably slightly hypocercal, with fulcra but without real lepidotrichia, its sides being covered by ordinary scales.

From the observations reported we thus find that *Drepanaspis*, though it is much specialized in several respects, is nevertheless very closely allied to the *Pteraspidae*.

Recently WOODWARD (1920, pp. 30—31) has referred the upper Devonian form *Phyllolepis* to the *Drepanaspidae*. And as can be seen from text-fig. 91, there are certainly characters which perhaps may suggest a relationship between this form and *Drepanaspis*. Thus the head and a considerable anterior part of the trunk are broad an depressed and provided with a carapace on the dorsal side of which we can distinguish several plates which somewhat resemble the dorsal plates of *Drepanaspis*.

On the other hand the carapace of *Phyllolepis* differs rather much from that in *Drepanaspis* for we find that the cornual plates (*C*) are developed as strong spines and that the dorsal median plate and the ventral plate project far backwards beyond the cornual plates.

The caudal region was probably without scales but had a partly ossified axial skeleton.

Where the eyes were situated and how the gills opened outwards is so far unknown. Likewise nothing seems to be known of the microscopic structure of the exoskeleton.

Since *Phyllolepis* both is imperfectly known and obviously differs in important features from *Drepanaspis*, it may be very much doubted whether it really pertains to the *Heterostraci* at all. In fact with the slight knowledge we have of it at present I find it very difficult to understand where it may have its nearest allies.

Apart from *Phyllolepis*, the relationships of which still remain very uncertain, we thus find that the *Drepanaspidae* in all respects are closely allied to the *Pteraspidae*, so closely even that they must have been derived either from common ancestors with these or from the oldest primitive forms among them.

Family Coelolepidae.

With regard to their general shape the *Coelolepidae* were ray-like and they were certainly adapted to a benthonic mode of living (text-fig. 92).

Their exoskeleton consistes, as is well known, exclusively of placoid scales, very much resembling the placoid scales of the Elasmobranchs.

Text-fig. 92. *Thelodus pagei.* Dorsal aspect. After TRAQUAIR (1899 b) 4/1.

ibr, interbranchial ridge; *ocr*, occipital region; *oes*, opening for the oesophagus; *orb?* possible orbit.

The eyes were small and situated exactly as in the *Pteraspidae* and *Drepanaspidae.* And the mouth and the external opening of the olfactory organ had certainly also similar positions as in these.

The endoskeleton must have consisted of a rather solid tissue, since in one specimen of *Thelodus pagei* there are distinct impressions of the endocranium and visceral endoskeleton. As far as can be judged this tissue must have been cartilage, perhaps strengthened in places by very thin perichondral bone-layers.

Text-fig. 92 is a copy of the figure given by TRAQUAIR (1899, b; pl. 39) of the very remarkable specimen of *Thelodus pagei* just referred to, which shows impressions of the endocranium and visceral endoskeleton. As we see in this figure, it is at once obvious that the endocranium and visceral endoskeleton must have been continuous with each other as in the Cephalaspids, and that the visceral endoskeleton, as in them, was not subdivided into branchial arches but formed a continous skeletal mass.

The longitudinal ridge which is denoted by the letters *ocr* in text-fig. 92, might perhaps at the first glance be taken for a cast of a groove corresponding to the aortal groove of the *Cephalaspidae*; but such an opinion is not in harmony with the fact that the ridge in question is so wide and in addition gets so rapidly narrower backwards. In fact, therefore, this ridge must be interpreted as the occipital region of the endocranium; and thus the *Coelolepidae* had a very long occipital region, like the *Pteraspidae.* The otic region is not shown, but it is presumable that it too was of the Pteraspidean type; and it is quite clear that this is the case with the orbitotemporal and ethmoidal regions too.

The visceral endoskelon evidently consisted of an antero-lateral part and a posterior part, of which the latter corresponded to the postbranchial wall of the Cephalaspidae and, like that, was perforated by a big foramen (*oes*, text-fig. 92) for the oesophagus. There are distinct traces of interbranchial ridges (*ibr*, text-fig. 92), and everything indicates that the gills were mesodermal ones of the same type as in the *Osteostraci*, *Anaspida* and *Pteraspidae*, i. e. that they were more or less sac-like. They numbered at least 7 and were probably a few more. How they opened outwards is unknown so far, since no indications of external branchial openings have been found with certainty hitherto. But this much is certain, that, if there was a common external opening for them, this must have been situated approximately as in *Drepanaspis*. If on the other hand, they opened outwards independently of each other it seems likely that their external openings lay on the ventral side, as in the *Cephalaspidae*. If the former alternative were true, the so-called "pectoral fin-flaps" would obviously be homologoues mainly to the postero-lateral corners of the carapace of the *Drepanaspidae* and would therefore only with their postero-medial parts correspond to the shoulder-girdle; and there would of course be no traces of pectoral fins. If, on the other hand, the second alternative were true the so-called "pectoral fin-flaps" would correspond both to the shoulder-girdle with the cornu and to the pectoral fins of the *Cephalaspidae,* and POWRIE (1869, p. 299) and TRAQUAIR (1899 b, p. 599) would be right in their suggestions as to this question.

According to WOODWARD (1920, p. 29), there are in *Thelodus* also undoubted indications of stout haemal spines in the vertebral column.

From what we know at present concerning them we cannot be in doubt any longer that the *Coelolepidae* are at the same stage of organisation as the *Pteraspidae* and *Drepanaspidae* and that they agree with these in most of their chief characters known hitherto. They differ, however, distinctly from the *Pteraspidae* and *Drepanaspidae* in one chief character: the development of the exoskeleton.

TRAQUAIR in his preliminary report in 1898 (1898, p. 74) on the fine *Coelolepidae*, just discovered at that time in Scotland, advanced the opinion that the *Coelolepidae* were altogether primitive, and this opinion he probably held also in his paper on *Thelodus pagei* (1899 b). Somewhat later, however, he had entirely changed his mind in this respect (TRAQUAIR 1899 c, pp. 843—844), as he then maintained that the *Coelolepidae* were highly specialized forms. But despite this he still considered them to be primitive with regard to the degree of development of the exoskeleton and so he did also in 1900 (pp. 772—774). This opinion — that the exoskeleton of the *Coelolepidae* is in primitive stage of development — has later on been adopted by KEMNA (1903, pp. 363—364), GOODRICH (1909, pp. 195—196) and most other writers. In reality this opinion has hitherto, under the influence of the current theory of the origin of the exoskeleton from fused placoid scales, been taken almost as a matter of course, and the reasons for and against it have hardly been subjected to a serious discussion.

To me, on the contrary it seems very likely that the exoskeleton of the *Coelolepidae* is the result of a regressive process of development, i. e. that it is in a very reduced state and that it originally consisted of bone of a similar type as in the allied forms — the *Pteraspidae* and the *Drepanaspidae.* The reasons which may be alleged for my opinion in this case are as follows.

1. A tendency to subdivision and degeneration of the exoskeleton similar to that wich seems to have occurred among the *Pteraspidae* may probably have occurred also in other allied groups of forms — for instance in the *Coelolepidae.* And it is very conceivable that this tendency was stronger in certain of the groups than in others, and that the progress of reduction therefore very well may be thought to have proceeded at different rates in two groups such as the *Pteraspidae* and *Coelolepidae.*
2. The absence of cell-spaces in the exoskeleton of the *Pteraspidae* and *Drepanaspidae* is, as I have pointed out, with a high degree of probability, a secondary character. The ancestors of the *Pteraspidae* and *Drepanaspidae* must therefore, as far as can be judged, have had an exoskeleton which contained bone cells. Now since exoskeletal plates, which lack cell-spaces and which in most features are *Drepanaspis*-like are found in deposits as old as the Middle Ordovician (*Astraspis*), it is evident that the *Pteraspidae* and *Drepanaspidae* with the typical microscopic structure of their exoskeleton — that is without cell-spaces — range very far back and that their supposed ancestors with an ordinary cell-bearing exoskeleton must have lived in a still more remote time. Expressed in another way: there are strong indications that the ancestors of the *Pteraspidae* and *Drepanaspidae* had cells in their exoskeletal bone and that these ancestors lived at a time very much before the time in which the Coelolepidae appeared, probably in the lower Ordovician or perhaps even in the Upper Cambrian.

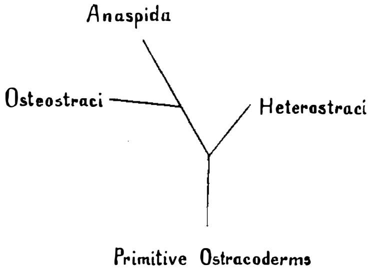
   Under these circumstances, when an exoskeleton of bone must be assumed to have been present already so early among the primitive ancestors of their nearest allies, it would obviously be very strange if the *Coelolepidae* themselves had not also originally been provided with a bony exoskeleton or at least had not descended from ancestors with such a skeleton. Further it is evident that the *Coelolepidae*, despite the fact that they are Silurian and lower Devonian forms, are not among the oldest Ostracoderms and that therefore their geological appearence cannot alone be held as an important fact for deciding whether certain of their characters are primitive or not.

3. The fact that the visceral endoskeleton and the endocranium in the *Coelolepidae* were continuous with each other and developed as in the *Pteraspidae*, *Drepanaspidae* and *Osteostraci* would be very difficult to explain unless we assume that the *Coelolepidae* originally had a carapace like the one in their nearest allies the *Pteraspidae* and *Drepanaspidae.*
4. If we assume that the endoskeleton of the *Coelolepidae* is in a primitive stage of development, we are forced to the conclusion that bone tissue arose independently in the exoskeleton of the *Osteostraci* and *Heterostraci.* But since, as has been pointed out, the supposed ancestors of the *Heterostraci* which lived during the the Cambrian or lower Ordovidium already had a bony exoskeleton there is much reason to believe that such a skeleton was present already in the common ancestors of the *Heterostraci* and *Osteostraci* and thus also in the ancestors of the *Coelolepidae.*

If now the Elasmobranchian-like character of the exoskeleton, as it seems and as I have maintained, are not primitive but the result of a process of reduction or degeneration, it is evident that the *Coelolepidae* must be very closely related to the *Pteraspidae* and *Drepanaspidae.* In any case the relationships between the *Coelolepidae*, on the one hand, and the *Pteraspidae* and *Drepanaspidae*, on the other, indicate clearly that the *Coelolepidae* must undoubtedly be referred to the *Heterostraci.*

* * *

From the brief account given of the different forms generally referred to them we find that, so far as we can judge, the *Heterostraci* constitute a natural unit. It is also clear from this account that the *Heterostraci* are agnathous and that they are allied to the *Osteostraci* and *Anaspida* and pertain to the same large category of lowly organized craniate vertebrates as these. On the other hand, we have been able to show above that in certain respects they are more primitive than the forms just mentioned, as for instance, with regard to the position of the olfactory organ, the more paired appearance of that organ, the position of the eyes, the construction of the rostrum and of the anterior part of the endocranium and finally also with regard to the disposition of the sensory canal system. Since with regard to the exoskeleton they have attained a rather high degree of specialization, however, they cannot have given rise to the *Osteostraci* and *Anaspida*, but it is fully evident that they must have evolved from a common ancestral form with these.



Text-fig. 93. Diagram showing the interrelationships of the chief groups of the fossil Ostracoderms.

From the account given here of *Heterostraci* it is further evident that these must belong to one branch of the Ostracoderms, while the *Osteostraci* and *Anaspida* pertain to another characterized especially by the excessive development of the upper lip and the secondary replacement of the naso-hypophysial opening to the dorsal side of the head. As far as can be judged at present, the interrelationships of the different groups of Ostracoderms would therefore be as is shown by the diagram in text-fig. 93.

Finally it has also to a certain extent been shown that the *Anaspida* and the *Osteostraci* among recent forms have their nearest relatives in the *Ptetromyzontidae*, while the *Heterostraci* among recent forms seem to be most akin to the *Myxinoids*. Whe shall have the opportunity to discuss this more in detail in the following chapter, which deals with the *Cyclostomata.*

These researches have thus led me to an opinion as to the systematic position and affinities of the *Heterostraci* that is entirely different from the one maintained by TRAQUAIR (1899 c, pp. 853—858) and KIAER (1924, pp. 122—123, 129).

Cyclostomata.

Among the *Cyclostomata* we shall first deal with the the Petromyzontids, which in several respects — particularly, however, with regard to their ontogeny -- are more completely known than the Myxinoids.

Petromyzontia.

Before I enter upon the Petromyzontids I should mention here that I have received much valuable information concerning their anatomy from Professor N. HOLMGREN of Stockholm, who is just preparing a work on their skeleton. In addition it should also be stated here that I have had the great privilege of going through in detail several of Professor HOLMGREN'S section series through *Petromyzon* and *Petromyzon*-larvae. And for his great courtesy in informing me thus of his unpublished results and for his kindness in placing at my disposal his material I wish here to express to Professor HOLMGREN my deepest gratitude. I also wish to thank Professor HOLMGREN both for the opportunities he has given me to discuse with him many of the problems which have arisen during the course of my researches into the *Cephalaspidae* and for the great interest he has taken in my work.

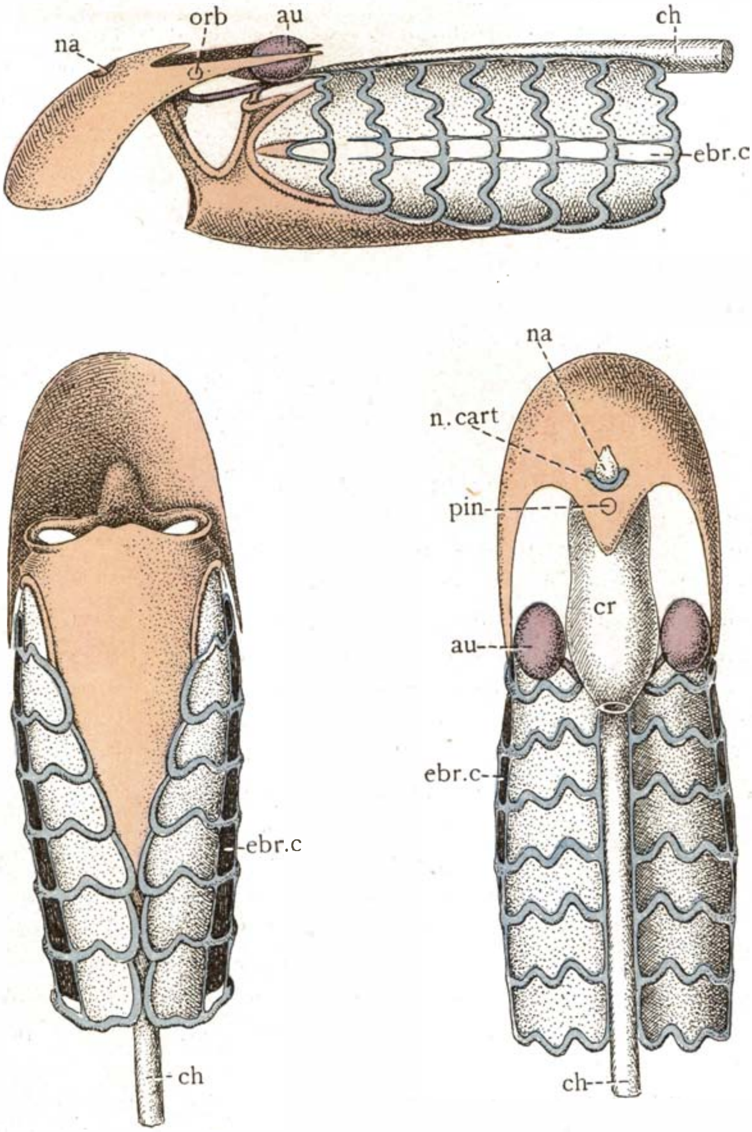
In the *Petromyzon*-larva, as has long been known, there occurs a sort of cartilage, generally termed muco-cartilage or mucous cartilage or in German Schleimknorpel (cf. SCHAFFER 1896, pp. 632—644; GASKELL 1900, pp. 565--577; 1908, pp. 331—339; SCHALK 1913). As this cartilage is of particular interest to us in this connection, it will be necessary to deal with it in detail; and it is all the more necessary to do so because its importance from a morphological point of view has hitherto not been realized, except to a certain extent by GASKELL (loc. cit).

Accordingly to GASKELL, the muco-cartilage of a *Petromyzon*-larva in a somewhat advanced stage of development has the distribution shown in text-fig. 94 of the present work. It would thus form a plate in the rostro-dorsal part of the head, which may be referred to as the rostro-dorsal plate, and a plate situated between the ventral ends of the 5 anterior branchial arches and extending from there upwards on each side in front of the branchial basket, a plate which may be termed the ventro-lateral plate. These two plates are said to be directly continous with each other at each antero-latero-dorsal end of the ventro-lateral plate, which in addition is firmly attached to the branchial basket. Below the place at which the two plates are connected with each other there is a gap between them in the restoration given by GASKELL (text-fig. 94 in the present work). But SCHAFFER, on the contrary, if I understand him correctly (1896, pl. 27, figs. 2—4), has found this gap filled out by muco-cartilage too. And according to information given me by HOLMGREN and as far as I can see myself, this is really the case. Thus the restoration published by GASKELL is certainly incorrect in this respect.

GASKELL (1908, p. 334) believed that he had found certain facts which appeared to him to indicate that the entire branchial basket behind the ventro-lateral plate in young larvae was covered on the outside by a layer of muco-cartilage; and that this is really the case has now been confirmed by HOLMGREN. But HOLMGREN has also found that this muco-cartilage, which for the sake of brevity we may call the branchial plate, disappears rather early, so that, except at certain spots in relation to the epitrematic and hypotrematic commissures, it is never found in larvae in more advanced stages of development.

The branchial plate of muco-cartilage is continuous anteriorly and ventrally with the ventro-lateral plate, and consequently the muco-cartilage of the larvae at this stage forms a continuous skeletal mass throughout the head and branchial region.

In addition it should be pointed out here that in specially stained section series in the possession of HOLMGREN the rostro-dorsal plate of muco-cartilage is seen to extend much farther backwards in the median parts of the head than was maintained by GASKELL.



Text-fig. 94. Endoskeleton of the head and branchial region of a *Petromyzon*-larva. The different kinds of cartilage shown in colours. Mucous cartilage red; soft cartilage blue; hard cartilage purple. After Gaskell 1908. According to N. Holmgren the mucous cartilage in the upper lip and in the anterior and ventral sides of the branchial region form a continuous mass so that the gap between them does not exist.

au, otic capsule; *ch*, notochord; *cr*, brain capsule; *ebr. c*, external branchial opening; *na*, nasal aperture; *n. cart*, nasal cartilage; *orb*, orbit; *pin*, pineal organ.

We thus see that muco-cartilage plays a very important part in the skeleton of the *Petromyzon*-larva and that it forms a continuous mass throughout the head and branchial region.

After this general orientation concerning its distribution we now proceed to a more detailed study of the muco-cartilage. The microscopic structure of this cartilage, which has been dealt with in a satisfactory way already by SCHAFFER and GASKELL, is not necessary to enter upon here.

The muco-cartilage is in places rather thick — as for instance most rostrally and around the olfactory organ, which is to a large extent surrounded by it — while in other places it is present only as a very thin layer. It lies on the whole close beneath the corium, with the basal layer of which it is in contact (text-fig. 95), extending from that inwards as far as the visceral musculature, which to a great extent invades its medial parts, so that these become more or less completely reduced especially most rostrally. Or to put it in another way: it fills the space between the corium and the visceral musculature, which invades and mostly destroys its medial parts. The segmental (somatic) musculature of the head and branchial region, on the contrary, is, as has been pointed out to me by HOLMGREN, situated within the muco-cartilage, so that in fact there is a layer of this both on the outside of it beneath the corium and on the inside of it. How these relations are between the muco-cartilage, on the one hand, and the visceral and segmental musculature, on the other, I have tried to elucidate in the somewhat diagrammatic text-fig. 95. Now since from what we know there is every reason to believe that the anterior segmental muscles of the Petromyzontids did not originally have their present extension forwards in the head but must have migrated forwards from a more posterior position (cf. KOLTZOFF 1901, pls. 6, 7; JOHNSTON 1905, pl. 5; cf. also text-fig. 38 in the present work which shows the anterior extension of the most anterior spinal motor nerve roots; cf. also GASKELL 1908; p. 337; DOHRN 1884—1891; HATSCHECK 1892; etc.) it is very conceivable that they originally were situated entirely behind the muco-cartilage. And we shall find that there are certain additional facts which point in the same direction.

As HOLMGREN has found, there is in the Petromyzontids a subepidermal and a subaponeurotic vascular plexus, just as in the *Osteostraci*; and it is now very interesting to find that the mucous cartilage lies just beneath the last mentioned one of these two plexus or so that this plexus falls within its most superficial part. It is also of importance to call attention to the fact that in its relations to the cranial nerves and vessels the mucous cartilage is exactly as certain parts of the endoskeleton of the *Osteostraci*. Thus, for instance, the rostro-dorsal plate is perforated by the profundus nerve, by the arteria facialis and by several veins.

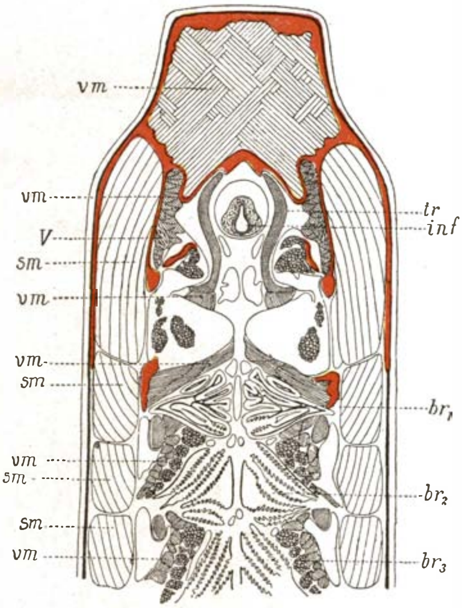
From its position and relations to the soft structures it is thus beyond question that the muco-cartilage of the Petromyzon-larvae was homologous with a considerable part of the endocranium and visceral endoskeleton of the Osteostraci and the other Ostracoderms. And it is remarkable to find that in its configuration as, a whole, it still retains the general outlines of the continuous Ostracoderm endoskeleton and that, like this, is has its visceral part continuous with the endocranial part. It is also worthy of notice here that it surrounds the mouth-opening and that there are no independent cartilages around this and that it thus also in this respect is very suggestive of the endoskeleton in the shield of the *Osteostraci*. Finally it deserves to be mentioned here that there are no independent lingual cartilages, their place being occupied by the ventral median part of the ventro-lateral plate of muco-cartilage.

Besides the plates of muco-cartilage just described the endoskeleton of the *Petromyzon*-larva is, as is well known, made up of other parts consisting of other sorts of cartilage. Thus there is a skeletal piece which earlier writers have considered to be the trabecula + the parachordal (text-fig. 94), but which SEWERTSOV (1916, 1917) rather recently has tried to interpret only as a parachordal, and an otic capsule, which both consist of hard cartilage. In addition there are branchial arches and a nasal cartilage (*na. cart*) which consist of soft cartilage. The branchial arches arise as independent elements, but become continuous with each other and with the neurocranium already in the larva. And it is further noteworthy that in those early larval stages in which the branchial plate of muco-cartilage is found they are situated close medially to this plate or perhaps even in such a way that they belong to it — a condition which makes it very probable, that they are of the same origin as this and that they are to be homologuized with the interbranchial septa and interbranchial ridges of the *Osteostraci* and other Ostracoderms. The nasal cartilage is to a great extent situated within the rostro-dorsal plate of muco-cartilage (cf. inter alia SCHALK, 1913, text-fig. 8); and the parachordalia of SEWERTSOV'S description reach so far forwards that most anteriorly they are at least partly surrounded by the said plate of muco-cartilage. Finally the otic capsule has hardly any direct connections with the muco-cartilage, but it seems not impossible that this may be a secondary phenomenon. In any case it can hardly be doubted that the skeletal parts now dealt with all have exact homologues in the endoskeleton of the *Osteostraci* and the other Ostracoderms, and that the skeleton of the *Petromyzon*-larva thus has retained other homologues of the endoskeleton of the Ostracoderms than the muco-cartilage.

In the *Petromyzon*-larva there is no cartilage in the posterior wall of the perichard, and the heart is therefore not enclosed in the branchial basket as in the adult but lies behind this, as it did in the Ostracoderms. Further, at least in the older stages of the *Petromyzon*-larva, the most posterior branchial arches are so long that they reach down to and meet their fellows of the opposite side in the median line on the ventral side of the branchial basket, whereas the anterior, ones on the contrary, become shorter in their ventral parts forwards, so that they gradually withdraw their ventral ends from the ventral ends of their fellows on the opposite side forwards. Because of this there arises between the ventral ends of the anterior branchial arches of both sides a gap which widens forwards, a gap which is entirely occupied by the ventral part of the ventro-lateral muco-cartilage plate. This gap obviously corresponds, at least in part, to the oralo-branchial fenestra of the *Osteostraci*, whereas the posterior branchial arches, which reach downwards and meet in the median line, occupy a similar position as the postbranchial wall of the *Osteostraci* and other Ostracoderms. It should also be pointed out here that in the *Petromyzon*-larva the external branchial openings of each side lie in a line which descends backward towards the ventral side of the animal, a condition which is well shown in certain of the figures given by PARKER (1883, pl. 8, figs. 1, 4). Accordingly with regard to the disposition of the external branchial openings the *Petromyzon*-larva is very suggestive of the *Anaspida* (cf. text-fig. 84 in the present work).

The characters of the branchial basket of the *Petromyzon*-larva just dealt with, together with the disposition of the external branchial openings, would already in themselves suggest that the Petromyzontids had been derived from forms with a rather short branchial region of a similar type as in the *Osteostraci*, or perhaps still more as in the *Anaspida*. But that this really must be the case is fully confirmed by the mode of development of the branchial basket and by the relations of the nerves. Thus KOLTZOFF (1901, pp. 432—435) has shown that the branchial basket during the ontogeny really grows backwards, while JOHNSTON (1905, pp. 195—196) has been able to establish that the relations between the truncus epibranchialis vagi and the somatic motor nerve roots are such that they can hardly be explained unless the branchial basket has secondarily been lengthened in a backward direction. JOHNSTON even arrives at the conclusion that the branchial basket originally did not reach further backwards than to the 10th somite. Accordingly we find that the Petromyzontids also with regard to the branchial basket originally must have been very much like the *Osteostraci* and *Anaspida*.

Before we proceed further in our account of the skeleton of the head and branchial region of the *Petromyzon*-larva, we have to consider the ontogenetic development of the olfactory organ and the hypophysis, a development which throws light on the nature of the anterior part



Text-fig. 95. Horizontal section through the anterior part of a *Petromyzon* larva. The figure shows the position of the mucous cartilage in relation to the visceral and segmental (somatic) muscles and to the corium. Mucous cartilage red. Chiefly after GASKELL.

cor, corium; *sm*, somatic muscles; *vm*, visceral muscles.

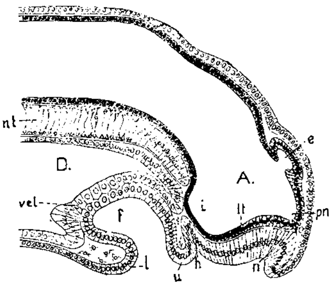
of the skeleton of the head. Above (pp. 323—325) we have already had the opportunity of dealing with this to a certain degree, but we shall now go a little more into details.

In larvae of 3 mm length (text-fig. 96) the head with the brain is much bent downwards with its prechordal parts, so that the lamina terminalis faces almost straight downwards (v. KUPFER 1905, p. 43). And it is specially noteworthy that the rostral tip of the head in this stage is formed by the ethmoidal region, that is by the cranium itself. Immediately externally and ventrally to the lamina terminalis lies in this stage the epidermis, which there consists of specially high cells and which presents two pits. The anterior one of these pits (*n*) is the olfactory pit, the posterior one (*h*), on the contrary, is the hypophysial pit, which later develops into the hypophysial sac. Both pits are involved in a common invagination and they are also both of them situated on the ventral side of the head, behind the rostrum and close in front of the mouth or more correctly the stomodaeum (*f*). In fact the hypophysial pit is separated from the stomodaeum only by a small fold (*u*) — the upper lip (cf. v. KUPFER 1905, pp. 42—43; PETER 1901, pp. 8—13; GOODRICH 1909, pp. 39—40; etc.). In the stages following next to the one just described (text-fig. 89) the olfactory and hypophysial pits are developed into the olfactory organ and the hypophysial sac respectively, and the invagination in which both of them were involved diminishes in diameter and it transformed into a space into which both open. The external opening of this space in its turn forms the common external opening of the olfactory organ and the hypophysial sac, on account of which it may be called the naso-hypophysial opening. The olfactory organ and hypophysial sac both retain, on the whole, their earlier relations to the anterior end of the brain, but since the longitudinal axis of this as well as of the head straightens out anteriorly by an upward swing of the prechordal part of the head as a whole, they gradually shift so that they become situated first in the rostral end of the head and then more dorsally. And as a consequence of this shifting, their common external opening, the naso-hypophysial opening, will face first antero-ventrally, then anteriorly and finally antero-dorsally. During the progress of straightening of the head the upper lip increases rapidly in size and swings forwards and upwards with its anterior end so that it projects in front of the naso-hypophyseal opening and forms the rostrum. Whereas the rostrum in earlier larval stages, as has been pointed out, is formed by the neurocranium — or more exactly by the ethmoidal region of this — it becomes thus in later stages instead formed by a structure of visceral origin. In still older stages the upper lip continues to increase in size, the preolfactory part of the head formed by it thus attaining a considerable length. The olfactory organ and hypophysial sac retain also during these oldest stages on the whole their original close relations to the anterior end of the brain unchanged, but the naso-hypophysial opening gets finally such a position that it faces almost straight dorsally.

The facts now advanced concerning the ontogeny indicate: (1) that the olfactory organ and the hypophyseal sac of the remote ancestors of the Petromyzontids lay so that they opened on the ventral side of the head, close in front of the mouth and behind the rostrum as in *Myxine* and the *Heterostraci*; (2) that the preolfactory part of the head in the Petromyzontids can not be homologuous with the rostrum and preolfactory part of the head in the Myxinoids and *Heterostraci* since these, as far as can be judged, are formed by the ethmoidal region (cf. PETER 1901, pp. 11—13; v. KUPFER 1905, pp. 23—58); and finally (3) that the muco-cartilage in the preolfactory part of the head, as far as to close in front of the olfactory organ, does not form part of the endocranium but that, since it is formed in the upper lip, it must pertain to the visceral endoskeleton.

As it has thus been established that by the excessive development of the upper lip and the displacement of the naso-hypophysial opening the anterior part of the head of the *Petromyzon*-larva undergoes such considerable transformations, it is not astonishing to find that it is difficult to recognize in it the homologous of the trabecles of other vertebrates (SEWERTZOV 1916, pp. 12—78). But that this condition would be primitive, as maintained by SEWERTZOV (1916, 1917), is entirely excluded.

According to what we have found from the above facts given the Petromyzontids are obviously unique among recent craniate vertebrates with regard to the position of the naso-hypophysial opening and the homologues of the preolfactory part of the head. On the other hand, it is easily seen that in these respects they agree very well with the *Osteostraci* and *Anaspida*. As has been shown, these had an unpaired olfatcory organ situated close in front of the brain and a hypophysial sac which did not communicate with the pharynx but ended blindly



Text-fig. 96. *Petromyzon*-larva, 3 mm long. Median sagittal section. After v. KUPFER 1905.

A, brain; *D*, alimentary canal; *e*, epiphysis; *f*, stomodaeum; *h*, hypophysial pit; *i*, infundibulum; *l*, lower lip; *lt*, lamina terminalis; *n*, olfactory pit; *nt*, notochord; *pn*, processus neuroporicus; *u*, upper lip; *vel*, velum.

beneath the infundibulum, exactly as in the *Petromyzon*-larva. In addition the olfactory organ and the hypophysial sac in these forms opened outwards through a common opening situated on the dorsal side of the head far behind the rostrum, just as in the Petromyzontids. And we are therefore able to conclude that the preolfactory part of the head in the *Osteostraci* and *Anaspida* must be homologous with that in the Petromyzontids and that, like that, it must have been formed by the upper lip.

Agreements of so special a kind as these between the Petromyzontids, on the one hand, and the *Osteostraci* and *Anaspida*, on the other, cannot possibly be considered to have arisen independently. Or to put it in another way: they cannot be parallelisms, but must indicate that the said forms are all very closely related to each other, in fact even so closely that they must pertain to a common branch of the Ostracoderms. And it should also be stated here that everything else that is known of the anatomy of the *Osteostraci* and *Anaspida* very distinctly points in the same direction.

Much has been written about the visceral skeleton of the *Petromyzon*-larva, but no very thorough analysis of it has, been published until rather resently by SEWERTZOV (1916, 1917). In the following brief account of it I shall chiefly follow SEWERTZOV, but since he has to a great extent overlooked the muco-cartilage I have, so far as that is concerned, to base my statement on GASKELL'S, SCHAFFER'S and HOLMGREN'S observations. Moreover it should be mentioned that, for certain reasons to be given below, I cannot adopt SEWERTSOV'S terminology with regard to the anterior visceral arches, but I shall employ the ordinary one.

After leaving the cranial cavity the typical branchial nerves, that is to say, the n. glossopharyngeus and the branchial nerves from the truncus epibranchialis vagi — pass first dorsally and entirely externally to the branchial basket. Well within the branchial basket each one of them continues downwards on the antero-medial side of an arch, behind the gill-sac corresponding to it. And it is very remarkable that each one of them has no pretrematic branch, but, on the contrary, a visceral branch which takes a ventro-medial course innervating a sense organs on the wall of the pharynx medially to its arch. The most anterior branchial arch related to a gill-sac is the one innervated by the n. glossopharyngeus. Anteriorly to that arch and its gill-sac — the first gill-sac — and thus anteriorly to the branchial basket there is in the elder larval stages, as we have seen, the lateral part of the ventro-lateral muco-cartilage plate (text-fig. 94). This part of the ventro-lateral muco-cartilage plate is in its dorsal half divided by a fenestra, the subocular fenestra, into two processes a posterior one, which ascends to the part of the parachordal situated ventro-medially to the otic capsule of its side, and an anterior one, which is continuous with the rostro-dorsal plate of muco-cartilage.

The former of these processes, which is rather narrow, has on its medial side two ridges in its longitudinal direction — one along the posterior and one along the anterior border (text-figs. 95, 97) — and both these ridges continue a certain distance ventrally beyond the processus on the medial side of the ventral half of the lateral part of the ventro-lateral muco-cartilage plate. Both the ridges are, at least in certain parts, very high and keel-like. And while the anterior one (*md*) lies in the velum and thus anteriorly to the spiracular or hyoid invagination (*sh*), the posterior one (*hb*) is situated behind this invagination, in the anterior wall of the first functionary gill-sac, but has similar relations to the visceral musculature as the branchial arches proper, as, for instance, the first branchial arch (br_1). The so-called r. mandibularis trigemini passes downward on the medial side of the former (*md*), whereas the n. facialis, at least according to SEWERTZOV, runs downwards mainly on the medial side of the latter.

From their positions and relations to the branchial invaginations and to the nerves and other soft structures SEWERTZOV arrives at the conclusion that the two ridges, together with the corresponding parts of the process on which they are situated, in fact are serial homologues to the branchial arches of the branchial basket and that the posterior one of them, together with the corresponding part of the process, is equivalent to the hyoid arch, while the anterior one with the corresponding part of the process represents the mandibular arch. And it seems beyond question that SEWERTZOV is right, at least in as much as that the homologues of the hyoid and mandibular arches have been moved towards each other, so that they form together the posterior process of the dorsal half of the lateral part of the ventro-lateral muco-cartilage plate. And this condition has perhaps given rise to the reduction of the gill-sac of the spiracular invagination. In the account below we shall refer to the ridges just described as the mandibular and hyoid ridges respectively.

The anterior process of the dorsal half of the ventro-lateral plate of muco-cartilage is incorrect in the restoration by GASKELL reproduced in text-fig. 94 in the present work. In reality it is continuous along its entire anterior side with the rostro-dorsal plate of muco-cartilage.[1] Close

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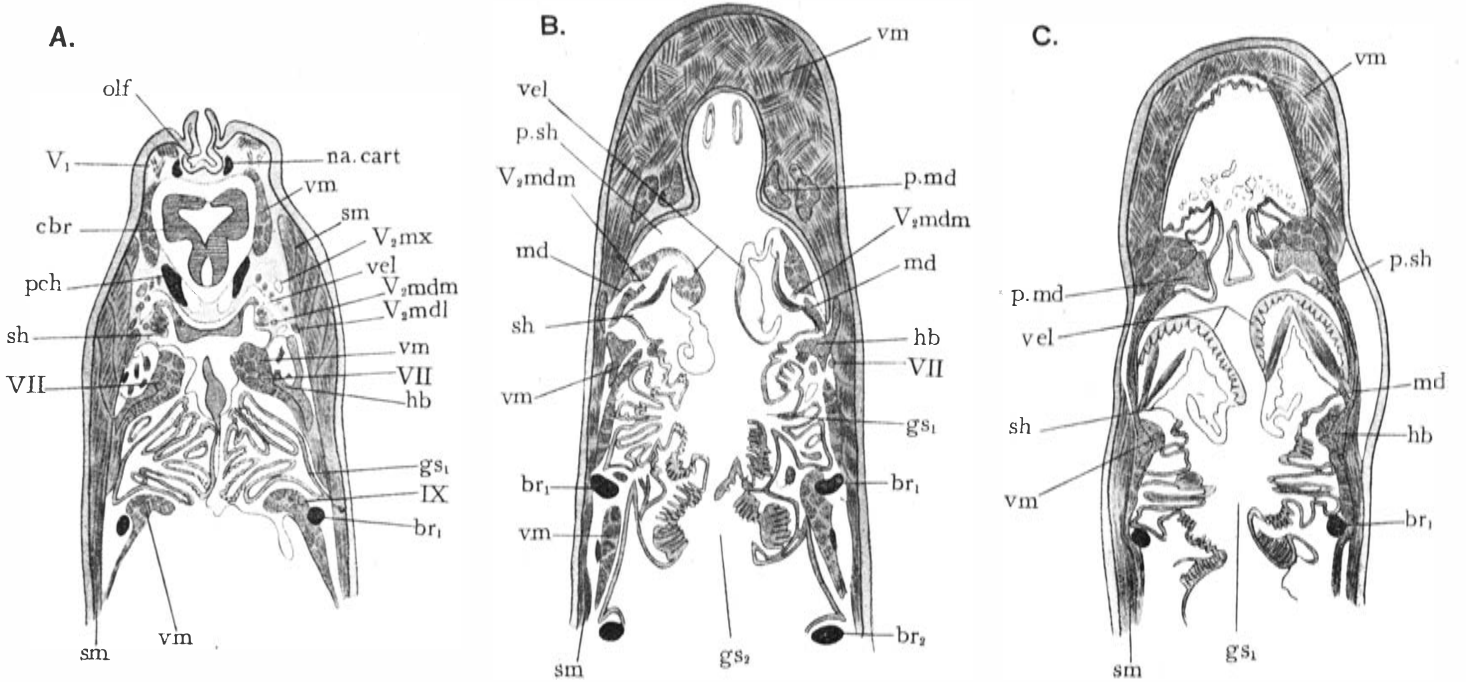
[1] This fact has not been observed by SEWERTZOV either.

anteriorly to the subocular fenestra by means of which it is separated from the posterior process of the same muco-cartilage-plate it has on its medial side a rather thick ridge, *pmd*, (text-fig. 97) which passes from above downwards and slightly posteriorly. This ridge lies medially to the so-called r. maxillaris trigemini (V_2 *mx*) and ventrally to the profundus nerve (V_1) and in addition in such a may that there is a very distinct invagination, the prespiracular or premandibular invagination *(psh)*, between it and the velum. Anteriorly to it follows the most rostro-dorsal part of the head formed by the rostro-dorsal part of the upper lip; thus the part of the upper lip that bounds the oral opening anteriorly and laterally. The visceral musculature, which so far anteriorly has strongly invaded the medial parts of the rostro-dorsal muco-cartilage (text-fig. 97), lies to a great extent laterally to the ridge within the rostro-dorsal plate; but it can hardly be doubted that this is a secondary condition, and that the most rostral visceral musculature originally lay medially to it. Despite the fact that this ridge, as we find, has not at all the typical relations of a branchial arch, SEWERTZOV nevertheless interpretes it as the homologue of a premandibular arch. It will be referred to here as the premandibular ridge.

This ridge is the only possible evidence of premandibular visceral arches which can be found in the *Petromyzon*-larva.

If we now pass to comparisons with the Ostracoderms, it is easely seen that the ridges of the *Petromyzon*-larva which have been described above as hyoid, mandibular and premandibular ridges are very suggestive of the interbranchial septa and interbranchial ridges, as, for instance, in the *Osteostraci* and *Coelolepidae* and that, on account of their relations to the skeleton otherwise and to the soft structures, they must be homologous with the correspondingly situated interbranchial septa + interbranchial ridges in the *Osteostraci*. Thus the hyoid ridge must be homologous with the second interbranchial septum + the second interbranchial ridge, and the mandibular ridge with the first interbranchial septum + the first interbranchial ridge, while the premandibular ridge presumably is equivalent to the prebranchial ridge (cf. text-figs, 4, 13, 36, 37).

In the *Petromyzon*-larva there follows, anteriorly to the premandibular ridge, a part of the upper lip which forms the anterior and lateral boundary of an anterior part of the oral cavity and the anterior and laterial boundaries of the mouth-opening. This part of the upper lip which is well seen in text-fig. 97 B anteriorly to the ridge *p. md*, occupies in most respects a similar position as the part of the upper lip of the *Osteostraci* that forms the boundary for the area *dpr* (text-figs. 4, 9—13, 36, 37); and, as far as can be judged, it is homologous with that part, though it is much more strongly developed. And accordingly we find that the upper lip of the *Petromyzon*-larva not merely as a



Text- fig. 97. Three horizontal sections through the head of a *Petromyzon*-larva. *A*, the most dorsal, *C*, the most ventral section. After SEWERTZOV 1916.

*br*₁, *br*₂, first and second branchial arches; *cbr*, brain; *gs*₁, *gs*₂, first and second gill-sacs; *hb*, hyoid ridge; *md*, mandibular ridge (muco-cartilage of the velum); *na. cart*, nasal cartilage; *olf*, olfactory organ; *p. ch*, parachordal; *p. md*, premandibular ridge; *p. sh*, prespiracular invagination; *sh*, spiracular invagination; *sm*, segmental (somatic) musculature; *vel*, velum; *vm*, visceral musculature; *V*₁, n. profundus; *V*₂, *mdl*, *V*₂, *mdm*, branches of the so-called r. mandibularis trigeminus; *V*₂, *mx*, the so-called r. maxillaris trigemini; VII, n. facialis; IX, n. glossopharyngeus.

whole but also with regard to details presents very striking agreements with the the most rostral part of the cephalic shield of the *Osteostraci*.

The most anterior branchial invagination that is provided with a gill-sac in the *Petromyzon*-larva is the one which is situated between the hyoid ridge and the first branchial arch. Anteriorly to this invagination there are, as has already been pointed out, two other branchial invaginations without gill-sacs, one of which, the spiracular or hyoid invagination (*sh*, text-fig. 97), lies between the hyoid and mandibular ridges, behind the velum, while the other one, the prespiracular or mandibular invagination (*psh*, text-fig. 97), lies between the premandibular and mandibular ridges, anteriorly to the velum. Now it is highly interesting that in the *Osteostraci* there are, as we have found, spiracular and prespiracular branchial fossae which both had gill-sacs. And contrary to what is the case in the *Petromyzon*-larva the *Osteostraci* thus had both spiracular and prespiracular gill-sacs. As far as can be judged from this, the Petromyzontids probably also orginally had gills developed in their spiracular and prespiracular branchial invaginations. In this connection it deserves also to be mentioned that probably the gill-sacs of the *Osteostraci* were more in accordance with those of the *Petromyzon*-larva than with those in the adult *Petromyzon*.

A special character of the gill-sacs of the Cyclostomes is that they are developed ontogenetically from the entoderm, while those of fishes, on the contrary, are of ectodermal origin (GÖTTE 1901; MOROFF 1902, 1904; SEWERTZOV 1917, pp. 532—545, etc.). On account of their position medially to the endoskeleton it is evident that we must assume that the gill-sacs of the *Osteostraci* and other Ostracoderms too all arose from the entoderm, save the first one, which evidently lies so far forward that it must have been formed by the ectoderm of the stomodaeum invagination exactly like that of the *Petromyzon*-larva.

SEWERTZOV has called special attention to the circumstance that in the *Petromyzon*-larva the branchial nerves and vessels as a rule pass on the medial side of the visceral skeleton, while in fishes they have their course instead on the outside of the visceral skeleton. In the *Osteostraci*, as well as in the Ostracoderms in general, they had similar relations, in the main, to the branchial skeleton as in the *Petromyzon*-larva.

The very unique and primitive features which occur in the visceral skeleton, particularly in the *Petromyzon*-larva but also in the adult Petromyzontids, led SEWERTZOV rather recently (1917, pp. 547—567) to the conclusion that the Petromyzontids, as well as the Myxinoids, must be primarily agnathous forms, as maintained by several writers. And that SEWERTZOV is right in this conclusion is now confirmed by the Ostracoderms which, as we have found, with full certainty have revealed themselves as agnathous craniate vertebrates. We are thus enabled to establish the fact that the Cyclostomes and Ostracoderms, as supposed by Cope so long ago as 1889 (pp. 852—853), pertain to a common branch of the craniate vertebrates which was in such a low degree of organization that its representatives had not acquired any jaws, a branch to which the term *Agnathi*, proposed by Cope, has to be applied.

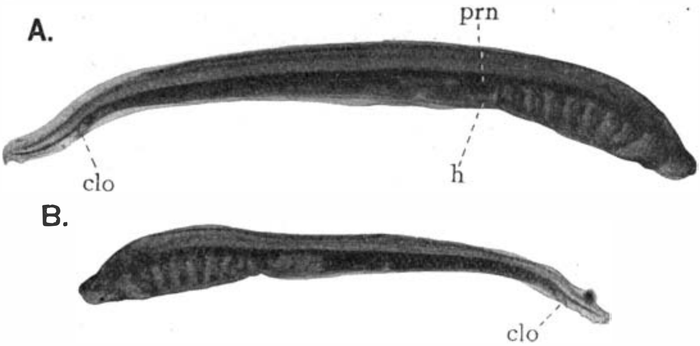
The arrangement of the visceral musculature in the *Petromyzon*-larva and the Ostracoderms, particularly the *Osteostraci* and *Anaspida*, must have had many features in common; and in any case it seems highly probable that the *Petromyzon*-larva in this respect must be nearer to the *Osteostraci* and *Anaspida* than are the adult Petromyzontids.

While in the adult Petromyzontids the pronephros is reduced completely, or almost completely, it plays, on the contrary, an important part in the larva (Felix 1904, pp. 156—166); and accordingly the larva is also in this respect much more in accord with the *Osteostraci*, which, as we have seen, throughout life had a persistent pronephros, than are the adult Petromyzontids.

Finally before we turn to the metamorphosis of the *Petromyzon*-larva attention should be called to the fact that in the young stages of this larva the caudal fin is very distinctly hypocercal (text-fig. 98), i. e. shaped so that the body axis, contrary to what is the case in the ordinary heterocercal caudal fin, is curved downwards. A hypocercal caudal fin also occurs in older stages of the *Petromyzon*-larva, although in them it is less distinct. It is very remarkable to find this type of caudal fin in the *Petromyzon*-larva since a similar caudal fin among lower vertebrates is know only among the Ostracoderms, in the *Anaspida*, and perhaps also in the *Drepanaspidae*. And it seems not improbable that this point of agreement between the *Petromyzon*-larva and the *Anaspida* may mean that the Petromyzontids are very closely related to the *Anaspida*, more closely than to the better known *Osteostraci*.

During the metamorphosis, as is well known, the *Petromyzon*-larva undergoes considerable changes not only with regard to the outer appearance but also with regard to the pronephros, the muscles, the vascular system, the skeleton etc., and in addition the rasping tongue and horny teeth arise. As has been mentioned already above, the pronephros disappears entirely, or almost entirely, while the musculature becomes more specialized. The vascular system is also subjected to rather considerable changes but as this changes will be dealt with separately below it is not necessary to enter upon them in this connection. Finally the skeleton is very much transformed too, and we shall nov pass to a brief account of the changes which take place in it.

What is first of interest to notice is that the muco-cartilage disappears entirely, being in part reduced, in part, on the contrary, transformed into most of the new cartilages which arise. How this procedure



Text-fig. 98. Two *Petromyzon*-larvae, showing distinctly the hypocercal caudal fin. A. 12 mm. long. B. 10 mm. long.
clo, cloacal opening; *h*, heart; *prn*, pronephros.

takes place in detail, however, is still very imperfectly known. According to BUJOR (1891, pp. 19—27) and SCHAFFER (1896, p. 645) the following of the new cartilages which arise would be formed from or within the muco-cartilage: the hyoideum (extrahyal, PARKER 1883), the cartilago mandibularis (epihyal + ceratohyal, PARKER), the subocular arch (pterygoid + ethmo-palatine, PARKER), the cartilago rhomboidea (upper labial III, PARKER), the cartilago dorsalis posterior (cornua trabeculae, PARKER), the cartilago dorsalis anterior (upper labial II, PARKER; semilunaris, FÜRBRINGER 1875), the cartilago annularis (annular, PARKER), the cartilago-lateralis (upper labial I, PARKER), the cartilago styliformis (lateral distal mandibular, PARKER), the cartilago copularis (median distal mandibular, PARKER), the cartilago glossa (basihyal PARKER) and perhaps also the cartilago apicalis (anterior basihyal, PARKER)[1]. Accordingly all the rostral and visceral cartilages anterior to the gill-bearing visceral arches would arise in or from the muco-cartilage.

SEWERTZOV (1916, pp. 63—78) has advanced the opinion that the anterior part of the subocular arch — the ethmo-palatine of PARKER'S description in 1883 — of the adult *Petromyzon* arises from the premandibular ridge of the larva and that as a consequence of this that part of the subocular arch represents the premandibular arch. Now since the cartilago rhomboidea and the cartilago lateralis of the adult Petromyzontids are more or less bar-like in shape and occupy a chiefly dorso-ventral position, and thus in their general shape and position are somewhat suggestive of the anterior part of the subocular arch, SEWERTZOV concludes that they represent two additional premandibular arches, so that altogether there would be in the adult Petro-

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[1] I have here adopted to some extent the terminology proposed by SEWERTZOV (1916), but chiefly the terminology recently proposed by TRETJAKOFF (1926 a, pp. 270—276).

myzontids not less than three premandibular visceral arches. The reasons brought forward by SEWERTZOV for this opinion may perhaps at the first glance be rather plausible, but if we take them into more serious consideration they appear anything but convincing. Thus it is very remarkable that in the larval stages there are no certain traces of more than one premandibular arch, and that in addition in the early larva only the three ordinary somites — the hyoid somite, the mandibular somite and the premandibular somite — can be found (cf. KOLTZOFF 1901). Moreover, as HOLMGREN has recently found, it is really the case that the premandibular ridge of the *Petromyzon*-larva does not give rise to the anterior part of the subocular arch but to the cartilago lateralis, that is to a cartilage situated immediately behind the cartilago annularis and the mouth. And accordingly HOLMGREN'S observation shows beyond question that there cannot be more than one premandibular arch in the Petromyzontids. In this respect too, therefore the Petromyzontids agree in reality very well with the *Osteostraci*, in which though they are more primitive with regard to the visceral skeleton than the Petromyzontids, there are, as we have seen, homologues only of one premandibular visceral arch and of one premandibular segment.

Besides the cartilages now dealt with, which all arise from mucocartilage, there are also others which appear during the metamorphosis and which are derived directly from connective tissue. Of this latter category of cartilages we shall consider here only one, the one which arises in the posterior wall of the perichard, the perichard cartilage.

The perichard cartilage unites anteriorly with the branchial basket so that, as has been pointed out above (pp. 339—340), the hear tin fact becomes situated inside the branchial basket. A homologue to this cartilage seems at first not easy to find in the Ostracoderms since these, as we have found, like the *Petromyzon*-larva, are without any correspondingly situated skeletal element and in addition have the heart situated behind the branchial basket. If, however, we undertake a little more detailed analysis of the conditions in the Cephalaspids, and in addition take into consideration the fact that the branchial region in the Petromyzontids has secondarily increased in length by a backward growth, it does not look quite impossible to explain the origin of the cartilage in question of the adult Petromyzontids and the reeson why the heart became enclosed by it in the branchial basket.

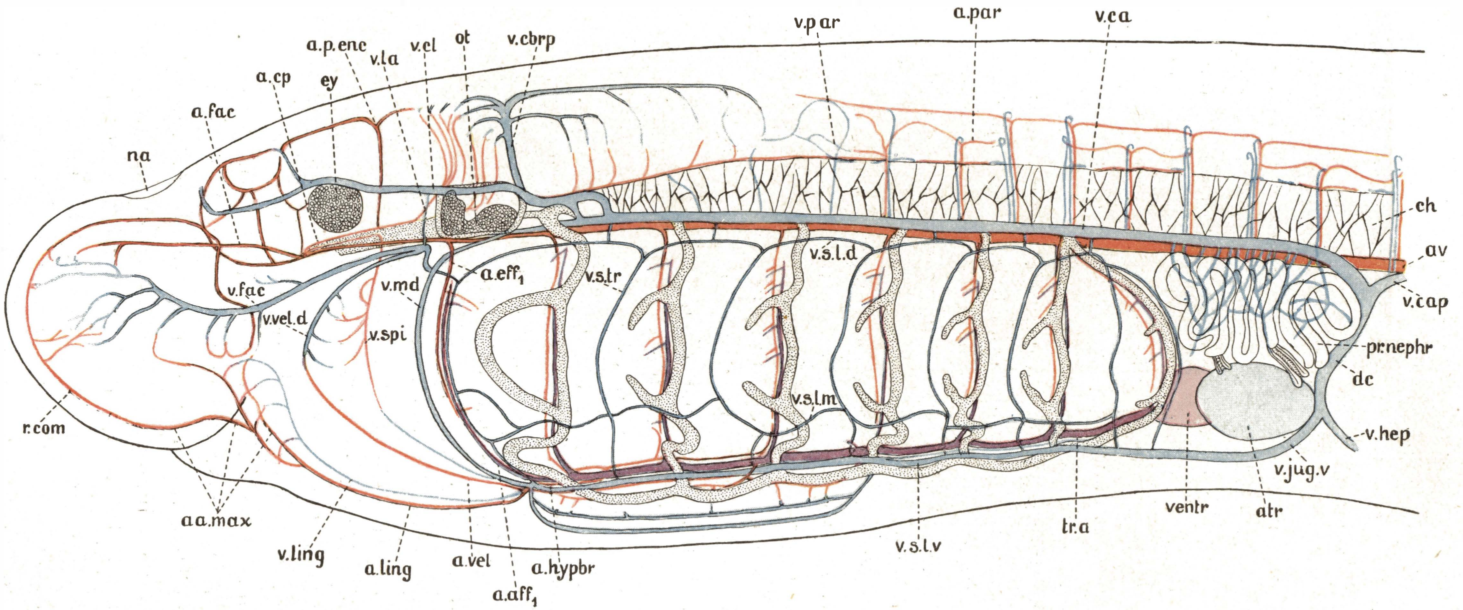
In the Cephalaspids the heart was, as we have seen, situated behind the ventro-median part of the postbranchial wall; and since at this place there is a rather pronounced pit, it was probably situated with its anterior parts in that very pit. Now if we imagine that in the Cephalaspids, when alive, the respiratory apparatus had begun to increase in length by a backward growth, the postbranchial wall would of course have had to push the heart backwards. And hence it is probable that the median part of the postbranchial wall, owing to the resistance offered by the heart, would have grown backwards more slowly than the lateral parts and that because of this the heart would have been completely surrounded on the lateral and posterior sides by the lateral parts of the postbranchial wall. If from such a presumed stage we imagine that the lateral parts of the postbranchial wall had coalesced with each other behind the heart and that the part of the same wall anteriorly to the heart had become reduced, the heart would evidently have been situated anteriorly to the branchial skeleton exactly as in the Petromyzontids. Accordingly we find that there is much reason to belive that in the adult Petromyzontids the peculiar position of the heart in relation to the branchial skeleton is a secondary character caused by the secondary extension of the branchial basket backwards.

It should further be mentioned here that during the metamorphosis of the *Petromyzon*-larva also the anterior branchial arches approach each other and unite with their ventral ends in the ventral median line just like the posterior ones, and that because of this the branchial basket loses much of its Cephalaspid-like character.

From what has been set forth here concerning its ontogenetical development it seems certain that the skeleton of the adult Petromyzontids in most respects is much more specialized than that of the larva. And in comparing the skeleton of the Petromyzontids with that of the Ostracoderms, therefore, we must not take that of the adult Petromyzontids into consideration but instead that of the *Petromyzon*-larva. Nevertheless it is, however, of much interest that even the adult Petromyzontids have retained certain primitive features in their skeleton. Thus their branchial basket, though being much perforated and made up only of bars of cartilage, is still a continuous structure, which in its turn is continuous with the endocranium. In addition they have in the subocular arch one more part of the visceral endoskeleton that has also retained its connection with the endocranium.

After this account of the skeleton, the branchial invaginations and the gill-sacs etc., we shall now pass to the brain and the nerves.

In the description of the *Osteostraci* above (cf. pp. 135—144, 303; textfigs. 15—17, 20—32; 82) we have already had occasion to compare the Petromyzontids and the *Osteostraci* with regard to the brain, and we have seen that there must have been many extraordinarily striking agreements between them in this respect. Thus we have been able to establish the facts that the *Osteostraci* had the hemispheres with the olfactory lobes, the diencephalon, the mesencephalon and the myelencephalon shaped almost exactly as in the Petromyzontids. And moreover we have found that the hypophysis of the *Osteostraci*, exactly like that of the Petromyzontids, formed a hypophysial sac which had an external opening in common with the olfactory organ but was without communication



Text-fig. 99. Blood-vascular system of the head and branchial region of a 7 mm. long *Petromyzon*-larva: After CORI 1906, with certain corrections after HATTA, 1922. The aorta and its branches red, the truncus arteriosus and its branches purple and the veins blue. Cartilage dotted.

aa. max, maxillary branches of the lingual artery; *a. aff*$_1$, first afferent branchial artery; *a. cp*, a. cerebralis posterior; *a. eff*$_1$, first efferent branchial artery; *a. fac*, arteria facialis; *a. hypbr*, hypobranchial artery; *a. ling*, lingual artery; *av*, aorta; *a. par*, parietal artery; *a. p. enc*, arteria plica encephali; *atr*, atrium; *a. vel*, velar artery; *ch*, notochord; *dc*, ductus cuvieri; *ey*, eye; *na*, naso-hyophyseal opening; *ot*, auditory organ; *pr. nephr*, pronephros; *r. com*, ramus labialis communicans; *tr. a*, truncus arteriosus; *v. ca*, v. cardinalis anterior; *v. cap*, v. cardinalis posterior; *v. cbrp*, v. cerebralis posterior; *v. cl*, v. capitis lateralis; *ventr*, ventricle; *v. fac*, v. facialis; *v. hep*, v. hepatica; *v. la*, branch connecting the v. capitis lateralis and the v. facialis; *v. md*, v. mandibularis; *v. par*, parietal vein; *v. spi*, spiracular vein (artery); *v. s. l. d*, v. superficialis longitudinalis dorsalis; *v. s. l. m*, v. superficialis longitudinalis media; *v. s. l. v*, v. superficialis longitudinalis ventralis; *v. s. tr*, one of the transversal superficial veins; *v. vel. d*, v. veli dorsalis.

with the pharynx. Finally, it may also be specially mentioned here that we are able to conclude that the right ganglion habenulae of the Cephalaspids was considerably bigger than the left one and in addition situated partly behind this — a character which occurs also in the Petromyzontids and the Myxinoids (cf. HOLMGREN 1919, pp. 55—65). But whereas the *Osteostraci* evidently must have had a big bilobate cerebellum the Petromyzontids, as is well known, have only a very slightly developed cerebellum. In the Myxinoids (text-fig. 42; cf. HOLMGREN 1919, pp. 83—87), on the contrary is a well developed bilobate cerebellum and as this is the case, there is in my opinion much reason to believe that the Petromyzontids originally also had a better developed cerebellum and that they also in this respect originally were very like the *Osteostraci*. HOLMGREN, with whom I have discussed this question and who has been occupied with detailed studies of the Cyclostome brain (1919) has informed me that he too considers it very probable that the Petromyzontids originally had a well developed cerebellum.

Also with regard to the spinal and cranial nerves there must evidently have been many very striking features in common between the Petromyzontids and the *Osteostraci*. Since above in the description of the Cephalaspids it was necessary to enter in detail upon these common features (cf. pp. 48—204 and and text-figs. 4, 13—30, 32, 36, 37 A, 38, 42, 43), it will be sufficient merely to enumerate them here. They are as follows: 1) the alternation of the spinal and spino-occipital nerves of the right and left sides; 2) the permanent separation of the dorsal and ventral roots of the spinal and spino-occipital nerves of each segment; 3) the presence of general cutaneous fibres in all the cranial nerves; 4) the presence of visceral branches of the branchial nerves for the supply of special sense organs; 5) the absence of pretrematic branches in the branchial nerves; 6) the position of the branchial nerves in relation to the visceral endoskeleton; 7) the mode of exit of the n. glossopharyngeus and of the n. vagus from the endocranium and in relation to the visceral endoskeleton, and further the course of the truncus epibranchialis vagi in relation to the visceral endoskeleton; 8) the mode of exit of the n. acusticus and n. facialis from the cavum cerebrale cranii and the mode of passage of the n. facialis through the otic capsule; 9) the mode of exit of the prootic lateralis fibres from the cavum cerebrale cranii in association with the n. facialis and the passage of these lateralis fibres to the otic capsule; 10) the course of the lateralis fibres for the trigeminus-profundus ganglionic complex forwards through the otic capsule and the position of the ganglion of these fibres in the postero-ventro-medial part of the orbit immediately in front of the otic capsule; 11) the great independence of the profundes nerve; 12) the mode of exit of the n. trochlearis and the n. oculomotorius from the cavum cerebrale cranii and the course of these nerves to the orbit; and (13) the position of the olfactory nerves very close to each other and the very inconsiderable length of these nerves.

There were also, however, certain differences between the Petromyzontids and the *Osteostraci* with regard to the cranial nerves. 1) Thus viscero-motor fibres are entirely absent in the profundus nerve of the Petromyzontids, while such fibres seem to have been present in the profundus nerve of the *Osteostraci.* 2) Moreover the trigeminus proper of the Petromyzontids breaks up into the so-called mandibular and maxillary branches already close distally to the trigeminus ganglion while the corresponding nerve in the *Osteostraci*, if we except the visceral branch, did not begin to subdivide into branches until very far distally and almost in the same way as the branchial nerves behind it. The n. trigeminus proper of the *Osteostraci* was therefore much more like the branchial nerves behind it than it is in the Petromyzontids. 3) Further in the Petromyzontids the n. glossopharyngeus passes entirely posteriorly to the otic capsule, whereas in the *Osteostraci* it traversed a postero-lateral part of the vestibular division of the labyrinth cavity. 4) Finally the Petromyzontids have no electric nerves while such were present in the *Osteostraci.*

It is not difficult, however, to conclude that, so far as the visceromotor component of the n. profundus is concerned, the *Osteostraci* were more primitive than the Petromyzontids, for if the n. profundus, as it seems to be, is the premandibular branchial nerve, it must of course, like the serially homologous branchial nerves behind it, originally have had a viscero-motor component. Further it is also probable that the *Osteostraci*, with regard to the mode of branching of the n. trigeminus proper, represent a more primitive stage than do the Petromyzontids, for it must of course be assumed that the n. trigeminus proper primarily branched in a similarly simple way as the other branchial nerves behind it and not as it does in the Petromyzontids. The different course of the n. glossopharyngeus in relation to the otic capsule in the *Osteostraci* and Petromyzontids, must certainly have been caused by a secondary increase in size of the auditory organ in the *Osteostraci*; and, as we know, a parallel to this is found in many fishes with a well developed auditory organ. Finally the presence of electric nerves in the *Osteostraci* must certainly be a specialization arisen within the group since electric organs are not known otherwise among the Ostracoderms. And we thus see that all the chief features by means of which the *Osteostraci* differed from the Petromyzontids with regard to the cranial nerves were either primitive and such that they might easily be thought capable of evolving in a *Petromyzon*-like direction or secondary and such that they may be considered to have arisen from more *Petromyzon*-like ones. Accordingly everything with regard to the brain and cranial and spinal nerves indicates that the Petromyzontids and the *Osteostraci* must be very closely allied to each other.

Above in this chapter on the Petromyzontids it has already been emphasized that an olfactory organ of the *Petromyzon*-type, and with an external opening situated exactly as in *Petromyzon*, occurred in the *Osteostraci*. And above I have also called attention to the very great morphological importance of this fact.

The Petromyzontids have, as we know, a membranous labyrinth of a strange type characterized among others by the absence of an external semicircular canal. In the *Osteostraci* we have now, as has been pointed out (pp. 77—94 above), found a group in which the membraneous labyrinth was without an external semicircular canal and in which the membraneous labyrinth in other respects was extraordinarily similar to that in the Petromyzontids.

The sensory canal system of the Petromyzontids (cf. STENSIÖ 1926, fig. 7; JOHNSTON 1905, pl. 5 and also text-fig. 38 in the present work; GASKELL 1908, text-fig. 84; etc.) differs with regard to its disposition on the head and branchial region rather much from that in the Osteostraci (cf. pp. 235—239, 306—308 above and text-figs. 76, 77 and 83); but on the other hand, as has been pointed out by the present writer (STENSIÖ 1926), it accords in this respect rather well with that of the Pteraspids. Now since, as we have found (pp. 238—239, 308), that of the *Osteostraci* seems to have been derived from a Pteraspid-like one, and thus evidently is more-specialized than that of Petromyzontids, it is fully evident that the Petromyzontids, though very nearly allied to the *Osteostraci* cannot have evolved from these, but from forms with a Pteraspid-like sensory canal system. Which these forms were — whether they were the common ancestors of the *Osteostraci* and *Anaspida* or the *Anaspida* it is so far impossible to decide.

It may also be noticed here that the presence of a sensory canal system of a Pteraspid-like type in the Petromyzontids and their nearest allies among the Ostracoderms seems to show that the Petromyzontids, the *Osteostraci* and *Anaspida* have evolved from primitive forms among the *Heterostraci*.

Finally we have to consider the blood vascular system, and concerning this we shall give a brief account first of the conditions in the *Petromyzon*-larva, then of those in the adult Petromyzontids, after this passing to a comparison with the *Osteostraci*. But since the blood-vascular system of the *Osteostraci* is known only in the head and in the adjacent most anterior part of the trunk, it is for the sake of comparison necessary to enter only upon the corresponding parts of the blood-vascular system of the *Petromyzon*-larva and the adult *Petromyzon*.

The blood vascular system of the *Petromyzon*-larva has been dealt with in detail mainly only by CORI in 1906 and by HATTA in 1922 (cf. also FAVARO 1908). And since the observations of these writers differ in many important points, it is not easy to give here a summary of their accounts and to judge of what is correct or not. It may, however, be pointed out that CORI based his researches on larvae of *Petromyzon fluviatilis*, while HATTA instead studied the Japanese form *Lampetra mitsukurii*, and that perhaps at least certain minor points of difference in their accounts may be due to this.

The heart of the *Petromyzon*-larva, as has already been mentioned, is situated behind the branchial basket, while the truncus arteriosus, the afferent and efferent branchial arteries all pass on the medial side of the visceral endoskeleton and thus inside the branchial basket. The truncus arteriosus (*tr. a*, text-fig. 99) goes forwards in the median line as far anteriorly as the posterior end of the thyreoidea, bifurcating there into a right and a left trunk, each of which continues forwards dorsally to the thyreoidea and somewhat laterally to the median line. From the truncus arteriosus issue on each side eight afferent branchial arteries, the most anterior one of which ascends in front of the first gill-sac medially to the hyoid ridge of the lateral part of the ventro-lateral plate of muco-cartilage, whereas each of the 7 posterior ones passes medially to a branchial arch. The most anterior one is thus the afferent branchial artery of the hyoid arch. According to HATTA, however, there is, in very young larval stages also a still more anteriorly situated vessel which, passing through the velum, connects the truncus arteriosus and the dorsal aorta with each other, a vessel which seems to be the serial homologue of the transversal vessels of the branchial region which during the corresponding stages connect the dorsal aorta and the truncus arteriosus, and which later give rise both to the afferent and efferent branchial arteries. This vessel through the velum may therefore be referred to as the mandibular vascular arch, and it is of interest since it indicates that in the Petromyzontids there primarely must have existed a spiracular gill-sac. The mandibular vascular arch, however, is soon transformed into the mandibular vein (*v. md*, text-fig. 99). Finally it should be mentioned here that HATTA believes that he has found traces also of a premandibular vascular arch.

According to CORI the conditions of the afferent and efferent arteries of the mandibular and premandibular segments are very different from what they are found to be by HATTA but as the thorough researches carried out by HATTA seem to warrant the belief that CORI is wrong in this respect, I shall not review his account here.

The aorta of the *Petromyzon*-larva (*av*, text-fig. 99) may be considered to be composed of caudal, abdominal, branchial and cephalic divisions, of which we shall deal here only with the last mentioned two. The branchial division may be defined simply as the one into which the efferent branchial arteries empty. And as is seen from text-fig. 99, it thus reaches from a transverse plane through the anterior ends of the otic capsules backwards as far as does the branchial basket. It is unpaired and lies throughout its extent in the branchial basket, straight beneath the notochord, and into it open the 8 efferent branchial arteries, the first one at the transition to the cephalic division. While the first efferent branchial artery ascends to the aorta medially to the hyoid ridge of the lateral part of the ventro-lateral muco-cartilage plate, each one of the seven efferent branchial arteries posteriorly to it goes upwards to the aorta medially to a branchial arch.

If I have understood Hatta correctly, there arises by the confluence of ventral branches from the efferent branchial arteries 2--4 a paired small ventral artery, the hypobranchial artery (*a. hypbr*, text-fig. 99) which goes forwards medially to the truncus arteriosus of its side rather close to the median line, slightly in front of the truncus arteriosus. The hypobranchial artery thus formed gives off an antero-dorsal branch into the velum, the velar artery (*a. vel*), beyond this point continuing forwards as the lingual artery (*a. ling*). This artery, when it arrives close behind the mouth, anastomoses with its fellow of the opposite side and breacks up into branches, the maxillary arteries, which continue antero-dorso-laterally and anteriorly as far as the lateral parts of the upper lip. One of these maxillary arteries, the ramus labialis communicans of Cori's description, goes laterally to the mouth-opening within the margin of the upper lip, according to Cori communicating most anteriorly with a branch of the rostro-dorsal system of arteries. And in this way the mouth opening is almost completely surrounded by an arterial ring. It is specially worthy of notice here that the maxillary arteries just described are, at least to a great extent, superficial vessels — i. e. they subdivide to a great extent into their terminal branches medially to the corium but laterally to the muco-cartilage. This fact is of great importance since it indicates beyond question that the maxillary arteries cannot be transformed parts of the prespiracular (premandibular) afferent branchial artery, as supposed by Cori.

The branches given off from the branchial division of the aorta are the parietal arteries, which ascend chiefly dorsally within the myosepta and which may anastomose with each other by collateral branches on a level with both the dorsal and the ventral borders of the medullary canal.

The cephalic division of the aorta — which, unlike the branchial division, is paired — is generally known as the dorsal carotid artery or as the internal carotid artery, terms which, as being misleading, will here be replaced by prootic aorta. The prootic aorta, as thus defined, goes forwards ventrally to the ventral cranial wall somehwat apart from its fellow of the opposite side and laterally to the notochord. It rather soon arrives on the medial side of the skeletal element of its side which has been considered by previous writers as the trabecula, but which, as already mentioned above, rather recently has been interpreted by SEWERTZOV as an anterior part of the parachordal.

In young larval stages HATTA finds that the artery here called the prootic artery gives off 3 parietal branches in a dorsal direction and that a fourth parietal artery is found issuing from it just at the point at which it merges into the branchial division. These four parietal arteries are said to ascend close to the brain, the first one medially to the profundus ganglion, the second one medially to the ganglion of the n. trigeminus proper, the third one medially to the roots of the n. facialis and the fourth one medially to the glossopharyngeus ganglion. And according to this position they seem to belong to the premandibular, mandibular, hyoid and glossopharyngeal segments respectively and thus to have a strictly segmental disposition. Unfortunately HATTA gives only very imperfect data concerning the topographical relations of all these vessels; nor is it possible from his figures to conclude exactly how they went in detail — for instance, in relation to the otic capsule etc. Like the parietal arteries in the branchial and abdominal regions, they give off dorsal and ventral collateral branches, which meet and join into a dorsal and a ventral longitudinal artery, the first of which lies dorsally to the ganglia of the cranial nerves, whereas the latter is situated in the angle between the brain and the notochord and develops later into the a. cerebralis posterior.

In later larval stages the first or premandibular one of the four parietal arteries just described retains its connection with the prootic artery of its side, and forms the cerebral artery proper, or, as it will be here called, the internal carotid artery, while the three posterior ones obliterate in their ventral portions, those portions which lie between the prootic artery and the posterior cerebral artery of their side. On the other hand the dorsal portions of the said posterior three arteries are retained as vertically ascending branches of the posterior cerebral artery, forming, if we take them in a rostro-caudal direction, in the main only the arteria plica encephali, the cerebellar artery and the occipital arteries respectively.

If, as it seems, HATTA is right as regards the ontogeny of the cerebral arteries we should evidently have in the Petromyzontids very primitive conditions with regard to the blood supply of the brain, and under the same supposition we should of course also be justified in expecting their ancestors to have been still more simply organized in this respect.

The internal carotid artery (the cerebral artery of HATTA's description), which thus seems to develop from the first or premandibular parietal artery, which incorporates parts of the three parietal arteries behind it, scends in older larval stages through the bottom of the cranial capsule to the fossa hypophyseos. Almost immediately after its origin from the prootic artery it bifurcates into an anterior branch and a posterior branch, the latter of which is the a. cerebralis posterior.

Close laterally to the point at which the internal carotid artery is given off from it, the prootic artery turns laterally as the arteria facialis (*a. fac*, text-fig. 99), crossing the parachordal of SEWERTZOV's description (the trabecula of other writers) on the ventral side, then turning antero-laterally and slightly dorsally and supplying the dorsal and dorso-lateral parst of the upper lip with arterial blood.

Neither CORI nor HATTA have considered the relations of the a. facialis to the rostro-dorsal plate of the muco-cartilage. In my sections series, however, I have been able to see that the a. facialis, rather soon after its separation from the internal carotid artery, enters the said plate of muco-cartilage, and that it in its further course passes within this until it breaks up into its terminal branches which lie immediately beneath the corium, between this and the muco-cartilage, forming a strong plexus there — a plexus which was briefly mentioned by MOZEJKO in 1912 (pp. 506—507) and which was called by him the plexus subcutaneous. We shall return to this plexus below.

Finally it should be mentioned that HATTA considers the facial artery to correspond, at least in part, to the premandibular vascular arch, a view which will be discussed below in the comparison with the Cephalaspids.

According to HATTA, a posterior branch issues from the a. facialis close to the internal carotid artery, a branch which goes along the outside of the parachordal, beneath the eye and the trigeminus ganglia. This branch has also been observed by CORI, but CORI in additon believes that he could trace it further peripherally and that it passed downwards into the medial part of the velum, on account of which he called it the v. spiraculi. Whether CORI or HATTA is right I am unable to decide; and it is also of no importance in this connection how it is with this branch.

As was mentioned above, there is a vascular plexus beneath the corium, a plexus which is not restricted only to the head but which occurs backwards on the entire body. But this plexus, which as has already been pointed out, is known as the subcutaneous plexus, seems, at least in the larval stages, to be best developed in those places where there is muco-cartilage. And attention must be called to the fact that it always in such places lies between the muco-cartilage and the corium. CORI and HATTA do not deal with it, but at least this much may, however, be gathered from their accounts that in the upper lip it is supplied with arterial blood from the arteria facialis and the anterior branches of the lingual artery. On the other hand the problem how the arterial blood arrives in the plexus in question farther back has not been studied, but it may be strongly suspected that, for instance, on the dorsal side of the head above the brain and the ears it is by superficial branches from the brain arteries, for, as is seen from text-fig. 99, there are otherwise no arteries by which it could be brought there.

HOLMGREN, who has recently studied the subcutaneous plexus more in detail than previous writers, has informed me that from it fine branches issue straight outwards to the outer parts of the corium, close beneath the epidermis, branches which anastomose there with each other by means of fine rami disposed concentrially with the stratification of the corium. A vascular plexus is thus formed superficially to the subcutaneous one, and close beneath the corium, a plexus for which the term subepidermal plexus will be employed.

Turning to the veins, we shall first consider the anterior cardinal vein or, as it also is often called, the v. capitis medialis. This vein (*v. ca*, text-fig. 99) is a paired vessel which from beneath the otic capsule passes backwards to the ductus cuvieri of its side. Throughout its exteni it goes close laterally to the aorta but slightly higher than this — in fact on a level with the lowest parts of the notochord. And while anteriorly to the first branchial arch — that is the glossopharyngeus arch — it is situated within the branchial basket it lies behind this arch instead dorsally to the branchial basket. Its relations to the muco-cartilage of the branchial basket, on the other hand, are not yet known.

The v. cardinalis anterior receives several tributaries, such as the v. capitis lateralis and a number of parietal veins. Further it is in connection anteriorly with the mandibular vein, and at least according to HATTA, by means of a branch with the vena facialis. Finally, it is also in connection with the superficial vein-system of the branchial region by means of transversal branches.

The vena capitis lateralis (*v. cl*, text-fig. 99) seems to begin antero-laterally and posteriorly to the olfactory organ, and it seems highly probable that it drains at least parts of that organ and the adjacent superficial parts of the upper side of the upper lip. It goes backwards to the orbit along the dorsal side of the n. profundus, receiving branches from the cavum cerebrale. Within the orbit it has its course dorsally to the eye and dorsally to the profundus and trigeminus ganglia, behind the orbit continuing dorsally to the otic capsule. Just before leaving the orbit, it is by means of a vertically descending canal (lettered *v. la*, in text-fig. 99) in communication with the facial vein. Just posteriorly to the otic capsule a rather considerable tributary, the vena cerebralis posterior (*v. cbrp*, text-fig. 99), which carries the blood from the posterior parts of the brain, opens into it, and behind this point it curves downwards and opens from the dorsal side into the v. cardinalis anterior close behind the first branchial arch. Besides the tributaries dealt with it certainly receives several fine veins which descend to it from the subcutaneous vascular plexus of the dorso-median and dorso-lateral parts of the head. Finally, it should be mentioned here that the v. capitis lateralis is considered to have arisen from anterior parietal veins.

Posteriorly to the v. capitis lateralis a great number of parietal veins descend to and open into the v. cardinalis anterior of their side. And concerning these veins it may be especially pointed out that anteriorly they are connected by collateral branches with the v. cerebralis posterior.

The mandibular vein (*v. md*, text-fig. 99) is a thick vein which descends from the v. cardinalis anterior to the vena jugularis impar on the ventral side of the branchial region. It lies deep below the epidermis, in fact probably medially (internally) to the posterior process of the ventro-lateral muco-cartilage plate. And concerning its position it is further to be added that it is situated approximately opposite the spiracular branchial invagination. As pointed out above, it has been shown by HATTA that it arises from the mandibular vascular arch, and in connection with the disappearance of the spiracular gill-sac it has thus, from having primarily been an arterial vessel been transformed into a vein, which secondarily has gained connection with the ventral vein system ventrally and with the v. cardinalis anterior dorsally.

The connections between the v. cardinalis anterior and the superficial system of veins of the branchial region will be dealt with below.

The antero-dorsal and antero-lateral superficial parts of the upper lip are drained by a vein of considerable size, the v. facialis (*v. fac*, text-fig. 99), which in its anterior parts is chiefly superficial, i. e. it brings the blood from the subcutaneous vascular plexus. It goes backwards and slightly dorsally, first superficially, then further postero-dorsally deeper medially owing to the fact that the segmented muscles which have extended forwards have pressed it inwards in this part. To a great extent, at least, it lies in the outer parts of or traverses muco-cartilage. Beneath the posterior part of the orbit it receives the v. veli dorsali of CORI's description (*v. vel. d*, text-fig. 99) from the velum, and immediately after that it makes a rather sharp bend in a ventral direction. Just at the bend a dorsally ascending fine branch *v. la*, which traverses the most posterior part of the orbit, puts it in communication with the v. capitis lateralis of its side. And, as we shall see, it is of importance that HATTA has found that the facial vein, as well as the vena veli dorsalis, arises from this branch during the ontogeny, and that CORI has been able to establish that during the earlier larval stages the blood from the v. facialis and the v. veli dorsalis empties by this branch into the v. capitis lateralis, while in older larval stages it is not constantly carried that way. According to HATTA the facial vein unites in *Lampetra mitzukurii* with the mandibular vein shortly behind the branch *v. la*; but in *Petromyzon fluviatilis* on the contrary, according to CORI and DE BEER

(1924, text-fig. 38), it has no such connection with the mandibular vein, but is instead continuous with the dorsal longitudinal one of the superficial veins of the branchial region. Concerning the v. veli dorsalis it must be added here that CORI and HATTA have paid no attention to its course in relation to the muco-cartilage. I too have been unable to establish anything with certainty in this respect, but since this vein, as has been pointed out, develops ontogenetically from the same primordium as the v. facialis, it can hardly be doubted that, like this, it must belong to the category of superficial veins, and that, at least primarily probably, it had a superficial position, though later on by the forward-growing segmental muscles it has been forced to occupy a deeper position.

The ventral side of the head and branchial region of the *Petromyzon*-larva is drained by the unpaired lingual vein (*v. ling*, text-fig. 99) and by the likewise unpaired v. jugularis impar which in reality forms the straight backward continuation of the former. The lingral vein, if we first consider that a little more in detail, is a rather fine vessel, which begins close behind the mouth-opening, and which seems to carry the blood from those parts of the ventral and lateral sides of the head that are supplied by the lingual arteries and their maxillary branches. It goes backwards medially to the ventral part of the ventro-lateral plate of muco-cartilage until close in front of the branchial basket, where it communicates with the v. mandibularis. Behind this point it is called the v. jugularis impar.

The v. jugularis impar runs backwards in the ventral part of the branchial region medially to the branchial skeleton, behind the branchial basket continuing beneath the heart and finally opening into the sinus venosus. While, according to CORI, it has in *Petromyzon fluviatilis* no connections with the transversal superficial veins of the branchial region, it is said by HATTA to be in *Lampetra mitsukurii* in communication with several of these veins. And in addition, while in *Petromyzon fluviatilis* CORI has found that also one of the longitudinal superficial veins of the branchial region opens into the v. jugularis impar close behind the branchial basket, this is, if HATTA is right, not the case in *Lampetra mitsukurii.*

The superficial system of veins of the branchial region, that has already been referred to, lies superficially to the branchial arches and segmental muscles close beneath the corium, and, as is shown by its position, it obviously drains the subcutaneous vascular plexus of this region. It consist of longitudinal and transversal veins. In *Petromyzon fluviatilis* (text-fig. 99) there are, according to CORI, 3 longitudinal veins and 8 transversal veins, whereas in *Lampetra mitsukurii* HATTA describes only two longitudinal veins but 8 transversal veins. Both in *Petromyzon fluviatilis* and in *Lampetra mitsukurii* the most dorsal longitudinal vein (*v. s. l. d*, text-fig. 99) runs rather far dorsally to the series of external branchial openings and is by segmentally disposed small transversal veins in communication with the v. cardinalis anterior of its side. The longitudinal vein following next ventrally (*v. s. l. m*, text-fig. 99) passes, both in *Petromyzon fluviatilis* and in *Lampetra mitsukurii*, in a similar way but somewhat ventrally to the series of external branchial openings. In *Petromyzon fluviatilis* it is called by CORI the v. superficialis longitudinalis media. The third one, which is present in *Petromyzon fluviatilis* but not in *Lampetra mitsukurii*, has its course approximately along or slightly above the level of the dorsal (dorso-lateral) margin of the commissures between the ventral ends of the branchial arches of its side and is thus a ventral vessel. In virtue of its position it was called by CORI the v. superficialis longitudinalis ventralis (*v. s. l. v.*), and it was said by CORI to be in connection with the mandibular vein anteriorly to the branchial basket and with the v. jugularis impar posteriorly to the branchial basket. Finally the transversal superficial veins (*v. s. tr*, text-fig. 99) which connect the longitudinal superficial veins run dorso-ventrally and thus transversally. With two exceptions — the most anterior one, which passes in front of the glossopharyngeal branchial arch, and the most posterior one, which passes behind the most posterior branchial arch — the transversal veins have their course between two adjacent branchial arches and accordingly they have a distinctly segmental disposition. While in *Petromyzon fluviatilis* all of them end ventrally in the ventral superficial vein, in *Lampetra mitsukurii* most of them reach down to and open into the v. jugularis impar.

In dealing with the superficial veins of the branchial region it should be mentioned that also in the trunk there is, at least in the adult Petromyzontids, a system of transversal metamerically disposed superficial veins and in addition in places also longitudinal superficial veins (cf. MOZEJKO 1912).

Finally concerning the vein system of the *Petromyzon*-larva attention should be called to the fact that in early larval stages the ductus cuvieri of both side is of equal size, but that in later larval stages the left one gradually decreases in size, finally entirely obliterating. And as a consequence of this the vein-system in the vicinity of the heart becomes asymmetrical developed.

After this brief account of the blood-vascular system of the *Petromyzon*-larva certain remarks may be added concerning the blood-vascular system of the adult Petromyzontids.

The blood-vascular system of the adult Petromyzontids differs from that in the larva particularly by the presence of numerous big vein sinus (MOZEJKO 1912; TRETJAKOFF 1926 b). Here, however, we shall deal only with a few of these vein sinus which are situated in the head.

Most anteriorly in the head of the adult *Petromyzon* there is a big sinus surrounding the mouth-opening. This sinus (*sas*, *sal*, *sai*, text-fig. 100), which is called by TRETJAKOFF the sinus annularis labialis, lies externally to the musculus annularis of FÜRBRINGER's (1875) description and close beneath the corium. It is in connection with the subcutaneous vascular plexus, and must evidently be considered as a specialized part of that plexus.

The mouth is surrounded not only by the sinus annularis labialis but also by another vein sinus with a much less calibre. This vein sinus, which is connected with the former, is described by TRETJAKOFF as the sinus interannularis. It lies between the musculus annularis and the cartilago annularis, and it thus has a deeper position than the sinus annularis labialis.

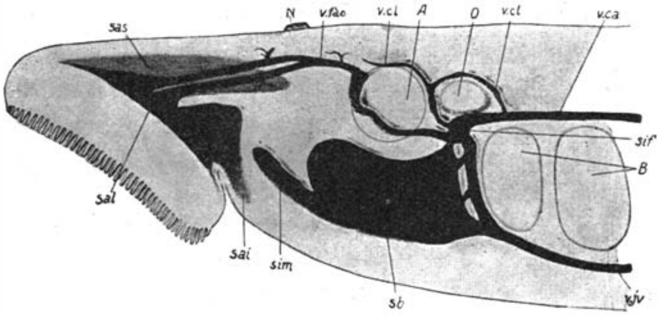
From the sinus annularis labialis arises the v. facialis (*v. fac*) as is well shown by text-fig. 100.

Among the numerous other vein sinus which occur in the adult Petromyzontids may here be mentioned the nasal sinus, which is in communication with the v. facialis, and the infracapsular (*sif*) and basilar (*sb*) sinus, the latter two of which are situated as shown by text-fig. 100. As is also seen from this text-figure, the v. capitis lateralis though, persisting, is in the adult evidently comparatively much less developed than in the larva.

Having given a brief account of the blood vascular system in the Petromyzontids, we can now turn to the blood-vascular system of the *Osteostraci*, particularly that of the Cephalaspids, comparing this with that of the Petromyzontids.

The heart of the *Osteostraci* was evidently situated similarly in relation to the visceral endoskeleton as that of the *Petromyzon*-larva in relation to the branchial basket. And moreover the truncus arteriosus of the *Osteostraci* certainly passed forwards medially to the endoskeletal element or elements which perhaps were situated in the soft tissue that closed the oralo-branchial fenestra, and accordingly it probably had similar relations to the visceral endoskeleton as that in the Petromyzontids. Finally it is also evident that the afferent and efferent branchial arteries of the *Osteostraci* all went medially to the visceral endoskeleton, exactly as the corresponding ones in the Petromyzontids. But while in the Petromyzontids the afferent and efferent branchial arteries in front of those pertaining to the hyoid arch do not persist as such, but are either transformed or have vanished, there in was the *Osteostraci*, as we have found, certainly mandibular (spiracular) afferent and efferent branchial arteries and in addition in the rostral artery at least a vestige of the premandibular (prespiracular) efferent branchial artery. And the *Osteostraci* were thus in this respect much more primitive than the Petromyzontids.

Concerning the efferent branchial arteries of the *Osteostraci* it is highly interesting to find that they arose from the adjacent halves of



Text-fig. 100. *Petromyzon.* Head and anterior part of branchial region showing the position of certain of the vein sinus. After TRETJAKOFF (1926 b).

A, eye; *B*, branchial sacs 1 and 2; *N*, naso-hypophyseal opening; *O*, otic capsule; *sai*, *sal*, *sas*, sinus annularis labialis; *sb*, sinus basilaris; *sim*, sinus intermuscularis; *sif*, sinus infracapsularis; *v. ca*, vena cardinalis anterior (v. capitis medialis); *v. cl*, v. capitis lateralis; *v. fac*, v. facialis; *v. jv*, v. jugularis impar.

two neighbouring gill-sacs, exactly as the corresponding vessels do in the Petromyzontids. In the Myxinoids, on the contrary, each gill-sac is drained by its own efferent branchial artery.

Before leaving the efferent branchial arteries attention should also be called to the fact that the efferent premandibular artery of the *Cephalaspidae* — the a. rostralis — has exactly similar relations to the visceral endoskeleton as the efferent branchial arteries behind it, i. e. it lies medially to the visceral endoskeleton. Now as in addition, as we know from the account of them, the *Cephalaspidae* had an arteria facialis which was homologous with the similarly named artery of the Petromyzontids, it is clear that this artery of the Petromyzontids cannot be a transformed part af the premandibular vascular arch, as maintained by HATTA.

Contrary to what is the case in the Petromyzontids, the aorta of the *Cephalaspidae* was an unpaired vessel throughout its extent. The branches given off from it were, as we have seen, the parietal arteries proper, the posterior encephalic artery (*a. cp*, text-figs. 44, 46), and the carotid artery. Concerning the parietal arteries proper we are able to conclude that they must have alternated with each other on the right and left sides, as in the Cyclostomes. And it is noteworthy that the posterior encephalic artery in this respect also was like a parietal artery and that in fact everything indicates that it was a transformed parietal artery. As we have seen, it entered the cavum cerebrale cranii from the ventral side medially to the place of exit of the glossopharyngeus and vagus roots; and on account of this fact it is very likely that it corresponded to the fourth parietal artery of the young *Petromyzon-*

larva, that is to the parietal artery of the young *Petromyzon*-larva, which, according to HATTA, gives rise to the occipital encephalic artery or arteries. The dorso-lateral superficial arteries, or at least the posterior ones of these arteries, may perhaps have been dorsal superficial branches of the occipital encephalic artery and thus of the supposed fourth parietal artery.

Under the assumption that the occipital encephalic artery of the *Cephalaspidae* really is the transformed fourth parietal artery, the third and second parietal arteries of the *Cephalaspidae* must obviously have lost their connections with the aorta. The postorbital superficial artery (*a. dsm*, text-figs. 44, 46, 49) was probably a dorsal superficial branch of the third parietal artery, while in the arterial branches which traversed the canals *ax* and ax_2 (textfigs. 20, 22, 27) we probably must have been concerned with branches of the second parietal artery.

The carotid artery (*a. car*, text-figs. 44, 46, 49) of the *Cephalaspidae* was probably the transformed first parietal artery. As is obvious from the description and the figures I have given of it, it seems to have been a rather wide vessel which arose from the aorta and thus had its connection with this retained. Rather soon it divided into a lateral and a medial branch, the former of which was the a. facialis (*a. fac*, text-figs. 44, 46, 47, 49), which perforated the preorbital parts of the endoskeleton and supplied the subaponeurotic vascular plexus in the anterior and antero-lateral parts of the cephalic shield, while the latter was the a. carotis interna proper. Both these branches were evidently in all important respects so much in accord with the correspondingly termed vessels in the Petromyzontids that it cannot be doubted that they really were homologous with these. And we thus find that with regard to the blood supply of the anterior superficial parts of the head the *Cephalaspidae* presented very great agreements with the Petromyzontids.

The subaponeurotic vascular plexus of the *Cephalaspidae* had a position exactly similar to that of the subcutaneous vascular plexus of the Petromyzontids. And since in addition it was supplied by similarly passing and homologous arteries as the last mentioned plexus it was certainly homologous with this. In addition the *Cephalaspidae* had also, like the Petromyzontids and the Myxinoids, a subepidermal vascular plexus.

The *Cephalaspidae* certainly had a paired, short anterior cardinal vein (v. capitis medialis; *v. ca*, text-fig. 50) which probably did not reach further forwards than to the postbranchial wall where it received the v. capitis lateralis of its side close postero-ventrally to the labyrinth. Accordingly these two veins joined each other externally to the branchial skeleton and close behind the labyrinth, exactly as in the Petromyzontids. The v. cardinalis anterior of the *Cephalaspidae* further received certain anterior parietal veins, a few anterior ones of which had their collateral branches transformed into the occipital vein sinus and thus by means of this were in connection with the v. cerebralis posterior. Similar connections — though not sinus-shaped but only very narrow ones — between the posterior parietal veins and the v. cerebralis posterior have been found by HATTA in larvae of Petromyzontids (HATTA 1922, pl. 22).

The v. capitis lateralis (*v. cl*, text-figs. 46—51) of the *Cephalaspidae* was, with regard both to its considerable size and to its course and position, very similar to the corresponding vein in the *Petromyzon*-larva. Thus, as we have seen, it arose from the subaponeurotic vascular plexus laterally and in front of the naso-hypophysial opening and passed backwards to the orbit, as a rule, chiefly dorso-medially to the n. profundus. The reader may further be reminded of the fact that, well within the orbit, it went rather high above the floor; further that behind the orbit it had its course dorsally or more correctly dorso-laterally to the labyrinth cavity; and, finally, that immediately behind the labyrinth cavity it left the neurocranium and curved downwards to unite with the v. cardinalis anterior. Like the corresponding vein in the Petromyzontids it drained the brain and the cavum cerebrale cranii; and in this connection it is especially worth while to call attention to the fact that there was a posterior cerebral vein (*v. cp*, text-figs. 46, 50), situated as in the Petromyzontids, that carried blood to it. Moreover, like the corresponding vein in the Petromyzontids, it received several small veins from above from the subaponeurotic vascular plexus of the dorsal side of the head. Finally, it had also lateral tributaries of considerable size, tributaries which are of much interest to us in this connection but which we shall not discuss until later. In this connection it should only be added that these lateral tributaries, as we have seen, were the dorso-lateral superficial veins.

As far as can be judged from its superficial position and its tributaries it is probable, as has already been mentioned above (p. 362), that the v. capitis lateralis of the *Cephalaspidae* pertained to the superficial system of veins. And if this was the case in the *Osteostraci*, it must obviously be the case in the Petromyzontids too. It should further be noticed here that the circumstance that it is well developed already in the *Osteostraci* indicates that the v. capitis lateralis must be a very old vessel. In full harmony with this is the fact that in the larvae of the Petromyzontids it appears strikingly early in the larva and is one of the chief veins of the head, while in the adult Petromyzontids it plays a much less important part (cf. DE BEER 1924, pp. 324, 327, text-figs. 36, 38). But it is difficult to judge from these conditions whether the v. capitis lateralis or the v. cardinalis anterior (v. capitis medialis) is the primitive head vein of the craniate vertebrates since, as we have found, the latter vein was present too already in the *Osteostraci* (cf. DE BEER, 1924, p. 339).

Besides the v. capitis lateralis the system of superficial veins of the *Cephalaspidae* consisted, as we have seen, of two longitudinal veins, of a number of transversal superficial veins, and of an annular labial vein sinus.

Of the two longitudinal superficial veins of the *Cephalaspidae* the most dorsal one was the marginal vein (*v. marg*, text-fig. 50), with its posterior continuation the marginal vein sinus (*vs. marg*). As this longitudinal superficial vein was situated dorsally to the branchial openings, it must have been homologous with the v. superficialis longitudinalis dorsalis of the Petromyzontids. The second longitudinal superficial vein of the *Cephalaspidae* was the ventral longitudinal vein (*v. slv*, text-fig. 50), and that vein must evidently have corresponded either to the v. superficialis longitudinalis medialis or the v. superficialis longitudinalis ventralis of the Petromyzontids. Whereas in the Petromyzontids the venae superficiales longitudinales (text-fig. 99) do not reach further forwards than approximately to a transverse plane through the anterior part of the otic capsules, in the *Osteostraci*, as we have seen, they extended almost to the tip of the head, a condition which probably is a primitive one, since the *Osteostraci* are not only very old forms but in addition forms which in general have retained much more primitive features in the visceral parts of the head than the Petromyzontids.

The transversal superficial veins of the *Cephalaspidae* consisted of the dorso-lateral superficial veins ($v.\,ls_1$—$v.\,ls_6$, text-figs. 46—51) and the ventral superficial transversal veins (v_1—v_{10}, text-fig. 50), all of which, as we have been able to establish, had a strictly segmental disposition. And it is not difficult to conclude that these veins together were comparable to and probably homologous with the transversal system of superficial veins of the Petromyzontids. More exactly, the dorso-lateral superficial veins probably corresponded to the parts of the transversal superficial veins of the Petromyzontids that are situated dorsally to the v. superficialis longitudinalis dorsalis, while the ventral transversal superficial veins were equivalents either of the middle divisions, or of these and the ventral divisions together, of the transversal superficial veins of the Petromyzontids.

While in the Petromyzontids the most anterior transversal superficial veins seem to belong to the glossopharyngeus segment there were in the *Cephalaspidae*, as we have found three veins of this kind in front of the one belonging to the glossopharyngeus segment — three veins corresponding to the hyoid, mandibular and premandibular segments respectively. As the head, according to the current view, is a structure arisen by the fusion and transformation of metameres, more or less like the abdominal metameres, we must of course assume that its vascular system primarily had a metameric disposition too. Now when in such lowly organized forms as the *Cephalaspidae* we find that the transversal superficial veins had a strictly metameric disposition, even in the most anterior parts of the head, this must of course be regarded as a primitive character. And everything thus indicates that the *Osteostraci* with regard to the presence of transversal superficial veins in the anterior part of the head were more primitive than the Petromyzontids.

In the Petromyzontids, as has been pointed out (cf. text-fig. 99), the dorsal divisions of the transversal superficial veins are all in connection with the v. cardinalis anterior (v. capitis medialis) of their side, while in the *Cephalaspidae,* on the contrary, they all emptied into the v. capitis lateralis. At first this differens seems perhaps to be rather important; but if we take into consideration the fact that the branchial region of the Petromyzontids has secondarily grown backwards and become much lengthened, it seems very probably that the dorsal ends of the transversal superficial veins have moved backwards too and have been secondarily connected with the v. cardinalis anterior, since there was no other vessel into which they could empty.

Finally it deserves to be pointed out here that, whereas the most dorsal parts of the transversal superficial veins of the Petromyzontids are in direct communication with the v. superficialis longitudinalis dorsalis, their supposed homologues in the *Cephalaspidae*, the dorso-lateral superficial veins, were connected with the marginal vein probably solely by means of capillaries. It seems very probable, however, that these conditions in the *Osteostraci* had been caused by the lateral electric field and accordingly that they were secondary ones. In this respect, therefore, as far as can be judged, the Cephalaspids were more specialized than the Petromyzontids.

The annular labial vein sinus of the *Cephalaspidae* lay externally to the visceral musculature, like the annular labial sinus of the adult Petromyzontids, and, like that, it was also in direct connection with the subaponeurotic vascular plexus. Moreover it lay chiefly on the outside of the endoskeleton, and thus it occupied a position almost exactly similar to that of the annular labial sinus of the adult Petromyzontids in relation to the annular cartilage. It is true that these facts seem to indicate that the vein sinus in question of the Cephalaspids was homologous with the similarly termed and similarly situated vein sinus of the adult Petromyzontids; but since in the larval stages of the Petromyzontids there is no annular labial sinus I do not, however, believe that this is the case. To me it seems instead more likely that in the annular labial vein sinus of the Cephalaspids and Petromyzontids we are concerned only with analogous structures. But it is evident that such a vein sinus could arise independently only in forms with a similarly developed subaponeurotic vascular plexus. In this connection it may also be added that, while the annular labial vein sinus of the Cephalaspids probably was drained by the ventral longitudinal superficial vein, the blood from the annular labial vein sinus of the Petromyzontids is carried away by the v. facialis.

The antero-lateral superficial parts of the head of the Cephalaspids from which the venous blood was collected by the dorso-lateral superficial veins 1—3 are in the Petromyzontids, as we have found, drained by the v. facialis and the v. veli dorsalis. Now since at least the v. facialis of the Petromyzontids is a superficial vein, and since in the Petromyzontids neither the transversal metamerically arranged superficial veins nor the longitudinal superficial veins extend so far forwards as this, there is evidently much reason to believe that the v. facialis and the v. veli dorsalis of the Petromyzontids represent together the much transformed three anterior dorso-lateral superficial veins of the Cephalaspids. More exactly, it seems as if the v. facialis arose from the dorso-lateral superficial veins 1 and 2 which in that case would have lost their connection dorsally with the v. capitis lateralis and instead, by means of commissures, joined with each other and with the third dorso-lateral superficial vein. The latter dorso-lateral superficial vein would have been transformed into the v. veli dorsalis and into the commissure which I have lettered *v. la* in text-fig. 99, and would thus have retained its connection with the v. capitis lateralis. And if we further take into account the facts that the commissure *v. la* in all respects corresponds exactly to the proximal part of the dorso-lateral superficial vein 3 of the Cephalaspids, that the v. facialis and the v. veli dorsalis ontogenetically develop from this commissure and that the blood from these two veins in young larval stages is regularly carried to the v. capitis lateralis through the said commissure (cf. p. 361 above), it seems beyond question that the v. facialis and the commissure *v. la* in question must represent at least the chief parts of the three most anter-dorso-lateral superficial veins of the Cephalaspids and thus be vessels arisen by transformations of the dorsal parts of the three most anterior transversal superficial veins. And that changes of the drainage of the superficial parts of the head can very easily take place is well shown in the Cephalaspids, in which, as we have seen, the posterior dorso-lateral superficial veins may join each other in several ways. Further evidence of this is also found in the rostral parts of the head of the Cephalaspids, for in certain cases, as we have been able to establish, the venous blood of the rostral parts of the head of the Cephalaspids went almost entirely to the rostral vein sinus and through this to the ventral superficial veins, while in other cases it was instead to a considerable extent brought backwards to the v. capitis lateralis by tributaries to the antero-dorso-lateral superficial vein.

The deeply situated ventral veins of the *Cephalaspidae* were probably, as in the Petromyzontids, an unpaired lingual and a likewise unpaired v. jugularis impar, which formed the direct posterior continuation of the former.

Finally it may be pointed out that the vein-system of the *Cephalaspidae* as a whole, like that of the adult Petromyzontids, was characterized by its big sinus formations.

As we find, the blood vascular system of the *Osteostraci* was of the same type as that of the Petromyzontids, and in addition it was in many respects very much in accord with that. And like the other systems of organs, therefore, it shows that the *Osteostraci* must be closely allied to the Petromyzontids. Though it was in many points more primitive than that of the Petromyzontids yet it had in a few respects attained a higher degree of specialication than that; and in this we have an additional evidence that the Petromyzontids cannot have been derived from the *Osteostraci.*

We have thus in this account been able to establish that the Petromyzontids are very closely allied to the *Osteostraci* and *Anaspida* among the Ostracoderms. Owing to the fact that the *Osteostraci* in certain details had attained a high degree of specialization, however, we cannot imagine the Petromyzontids to have descended directly from them. The *Anaspida* are too imperfectly known to be compared in detail with the Petromyzontids, but since they had a hypocercal caudal fin, and since we have found quite distinct traces of a similar caudal fin in the larvae of the Petromyzontids there seems to be some reason to believe that they perhaps might have given rise to the Petromyzontids. If this should not be the case the Petromyzontids must have envolved from the common ancestors of the *Osteostraci* and *Anaspida,* for in any case it is quite certain that they pertain to the same branch of the Ostracoderms as the *Osteostraci* and *Anaspida.*

The very greatly extended knowledge we now posess concerning their ancestry makes it is obvious that the Petromyzontids with regard to the skeleton must be highly specialized and degenerated forms. Further it is also clear that the absence of pectoral fins in them must be secondary, arisen by reduction. Finally it seems also not improbabel that the absence of an occipital region in them is a secondary feature too, a secondary feature which may very well be thought to be a consequence of the degeneration of the skeleton in general. In any case the conditions in the *Osteostraci*, *Anaspida* Petromyzontids and *Heterostraci* suggest that the presence or absence of an occipital region cannot in itself be sufficient to prove anything with regard to the stage of organization of a group.

Setting aside the features just considered and certain others of minor importance, however, the Petromyzontids have on the whole been found to remain in a primarily low stage of organisation and to be primarily agnathous forms, as first assumed by COPE.

Myxinoidea.

As the Myxinoids on the whole belong to the same special type of organisation as the Petromyzontids, it is beyond question that they are closely allied to the Ostracoderms. But while, as we have seen, the Petromyzontids, the *Anaspida* and the *Osteostraci* have the naso-hypophysial opening situated far back on the dorsal side of the head and the rostral parts of the head formed by the excessively enlarged upper lip, the Myxinoids, on the contrary, are characterized by the position of the naso-hypophysial opening decidedly ventrally and not so far in front of the mouth and by the fact that the ethmoidal region protrudes forwards as the rostrum (cf. PETER 1901, pp. 8—13; V. KUPFER 1905, pp. 24—58; cf. also pp. 323—325, 340—343 above in the present work). Since in addition their upper lip does not increase in size, the Myxinoids, so far as the anterior part of the head is concerned are much less specialized than the Petromyzontids, the *Anaspida* and the *Osteostraci*; and it is therefore easy to understand that they cannot have been derived from any of these groups. Instead of that, in the respects here in question they approach the *Heterostraci*; and it seems therefore rather likely that they may be more or less direct descendants from these. In this connection attention may also be called to the circumstance that in certain of the Myxinoids, e. g. *Myxine*, the mode of opening outwards of the gill-sacs is exactly as it must have been in the *Heterostraci* (cf. pp. 326, 329, 332 above).

Unfortunately the *Heterostraci* are still so imperfectly known that no detailed comparisons can be made between them and the Myxinoids.

The ontogeny of the Myxinoids is very imperfectly known, but it is nevertheless possible to see that it presents many points of interest (cf. DEAN 1899). First of all, it is very noteworthy that the embryos (text-fig. 101) are much flattened in a dorsi-ventral direction and have a rather short branchial region. Further it is clearly seen that the branchial region secondarily grows backwards and that the gill-sacs secondarily come to occupy their peculiar position very far back behind the head. And finally it is highly interesting to find that in certain stages (text-fig. 101 C) the general appearence of the embryo in a lateral view was very suggestive of a Pteraspid.

What is known so far of the ontogeny thus seems to indicate that the ancestors of the Myxinoids were benthonic, dorsi-ventrally flattened forms with a rather short branchial region, forms which, on the whole, must have had a shape similar to that of the Pteraspids among the *Heterostraci*.

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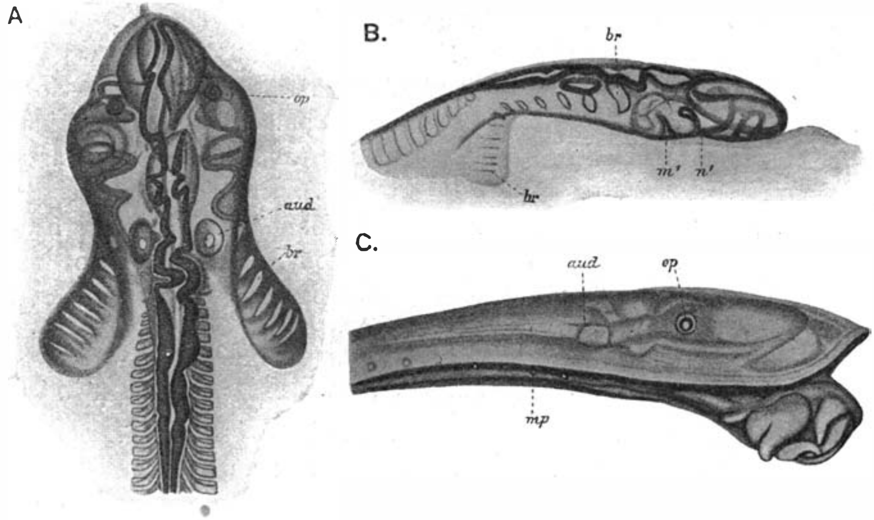


Text-fig. 101. *Bdellostoma.* Head and branchial region of three embryos. After DEAN 1899.

A dorsal view of an embryo with about 8 gill slits; B, lateral view of an embryo with about 13 gill slits; C, lateral view of an older embryo.
aud, auditory organ; *br,* branchial slits; *mp,* mucous pouch; m_1, region of the mouth; n_1, region of the nasal opening; *op,* eye.

From what has been set forth here it is evident that the Cyclostomes are very closely related to the Ostracoderms, so closely even that they must be included among the latter. Moreover it has been shown above that the Petromyzontids must pertain to the same large branch of the Ostracoderms as the *Osteostraci* and *Anaspida* and be derived either from the *Anaspida* or from the common ancestors of these and the *Osteostraci.* And finally from the account given above we have also found that the Myxinoids must be nearest allied to the branch of the Ostracoderms that comprises the *Heterostraci* and that they perhaps may be descendants of the *Heterostraci.*

Thus the Ostracoderms had already very early separated into two main branches, one of which includes the *Osteostraci*, *Anaspida* and *Petromyzontia*, while the other consists of the *Heterostraci* and *Myxinoidea.* To make it easy to refer to these two branches it will of course be necessary to name them and I therefore propose for the first mentioned branch the term *Cephalaspidomorphi* and for other the term *Pteraspidomorphi.*

The knowlegde which we now possess concerning their phylogeny and relationships shows that the *Petromyzontia* and *Myxinoidea* have degenerated in certain respects, as, for instance, with regard to the degree of development of the skeleton and the absence at least of pectoral fins and shoulder-girdle, but that otherwise on the whole they remain in a very lowly organized stage of evolution and that they are primarily agnathous forms (cf. SEWERTZOV 1917, pp. 547—567).

Finally it should be pointed out here that since a well developed bony skeleton was present already in the primitive agnathous craniate vertebrates, as in the Ostracoderms, such a skeleton must have arisen very early among the craniate vertebrates. And as this is the case, it is of course very likely that the ancestors of the gnathostomes had a bony skeleton too, and accordingly that a bony skeleton was not independently acquired by the different groups of lower Gnathostomes, as seems to have been generally assumed. Since in addition I have been able to show (STENSIÖ 1925 b, pp. 160—164, 187—189) that probably a bony skeleton was primarily present also in the Elasmobranchs, everything seems thus to indicate that such a skeleton really was inherited in the Gnathostomes from the agnothous craniate vertebrates.

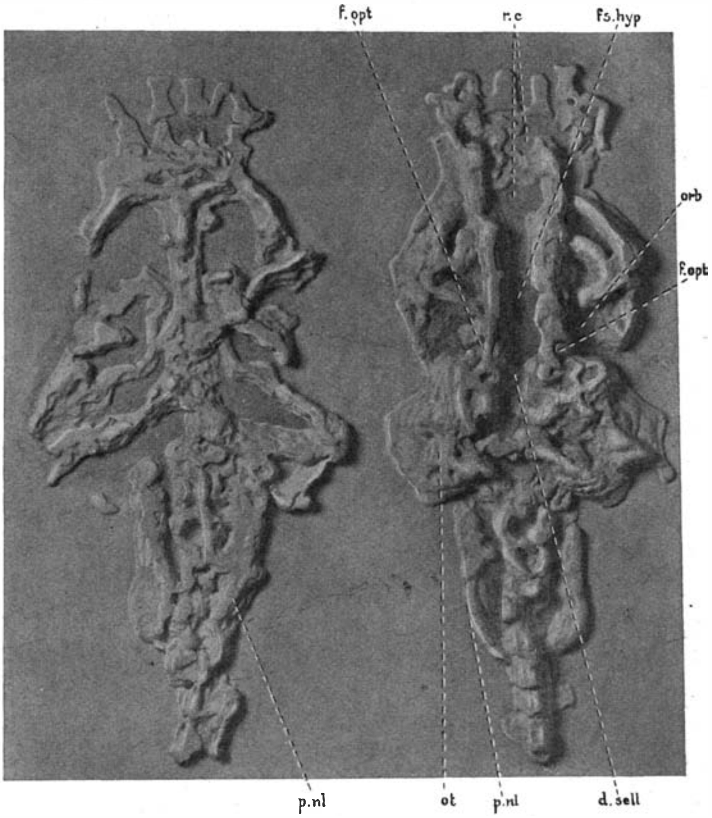
Palaeospondylus.

On account of its general Cyclostome-like appearance *Palaeospondylus gunni* has ever since its discovery attracted a very great interest and numerous papers have been published on it (TRAQUAIR 1890 b, 1893 d; 1894 b, c, d; 1897; GILL 1896 a, b; DEAN 1896 a, b; 1898; 1900; KERR 1900; SOLLAS 1904 a; etc.). But as it was a very small animal and as moreover the remains of it are always much affected by pressure in the rock our knowledge of it still remains very imperfect in many important respects, and it is therefore possible to enter here only upon certain of its characters.

The skeleton of *Palaespondylus* consists, in its present state of preservation, of a coal-like substance without distinct microscopic structure. Since the fishes, such as *Coccosteus decipiens*, which are found in the same rock with *Palaeospondylus* have their skeleton preserved as a similar coal-like substance, it seems probable that what remains of the skeleton in the fossil of *Palaeospondylus* also consisted of bone (cf. SOLLAS 1904, pp. 270—273).

The endocranium (text-fig. 102) is of a rather peculiar type and, like that of the Petromyzontids and Myxinoids, it has no occipital region but ends posteriorly with the otic region (*ot*, text-fig. 102).

The otic region, which is the broadest one of the regions of the head, encloses, according to SOLLAS, a paired labyrinth cavity which in the fossil state communicates with the cavum cerebrale cranii by means of a rather wide opening. The orbitotemporal region is short and is characterized by a paired latero-dorsally open fossa (*orb*, text-fig. 102), which must be the orbit. It is very noteworthy that this fossa, which will be referred to as the orbit, is provided with a floor which passes



Text-fig. 102. *Palaeospondylus gunni* TRAQUAIR. The skeleton of the head in ventral (A) and dorsal (B) view. Photograph of a copy of a model presented by Professor SOLLAS to the palaeontological institution of the University of Upsala.

d. sell, dorsum sellae; *f. opt*, fenestra optica; *fs. hyp*, fossa hypophyseos; *orb*, orbit; *ot*, otic capsule; *p. nl*, pronephros lamella; *r. c*, space occupied by the olfactory organ and the hypophysial sac.

over anteriorly into the ventro-lateral parts of the ethmoidal region. This last-mentioned region is more than twice as long as the orbitotemporal region and is therefore much longer than both the other regions of the endocranium together. Posteriorly on each side it has a broad lateral preorbital portion strengthened by two or three obliquely transversal ridges on the dorsal side, a portion which SOLLAS was inclined to interprete as a nasal capsule. Anteriorly the region forms the rostral end of the head, which, as is well known, is provided with short skeletal processes, called rostralia by SOLLAS. And it is noteworthy that these rostral processes seem to be arranged in such a way that they surround an antero-ventrally directed unpaired opening, which is situated in the rostral end of the head, (TRAQUAIR 1894 d, pl. IX, figs. 1, 2) and which leads into a big cavity (*r. c*, text-fig. 102) which we shall call provisionally the rostral cavity.

The cavum cerebrale cranii (text-fig. 102) is long and narrow and continuos anteriorly with the rostral cavity, as thus defined. Just at the transversal plane through the anterior ends of the otic capsules its floor suddenly descends to a lower level than posteriorly, so that there arises a fossa hypophyseos (*fs. hyp*, text-fig. 102) bounded posteriorly by a distinct dorsum sellae (*d. sell*). As far as can be understood, the fossa hypophyseos has a very considerable forward extension.

Close in front of the dorsum sellae the lateral cranial wall is perforated by a big foramen (*f. opt*, text-fig. 102), which leads laterally to the orbit. Since this foramen lies just laterally to the posterior parts of the fossa hypophyseos, it has an exactly similar position as the fenestra optica of the Cephalaspids and must, as pointed out by SOLLAS, have been traversed at least by the n. opticus.

From the position of the dorsum sellae and the fossa hypophyseos it is evident that the fore-brain cannot have been so long as to occupy the entire anterior part of the cavum cerebrale, still less the rostral cavity, but that the conditions must have been simply such that the olfactory organ was situated in the anterior part of the cavum cerebrale and that the rostral cavity was the duct which led outwards from the olfactory organ to the opening in the rostral end of the head surrounded by the rostral processes. To put it in another way: the fact that the cavum cerebrale anteriorly is continuos with the rostral cavity indicates that the olfactory organ was situated as in the Petromyzontids and Myxinoids, and opened outward with an unpaired duct in the rostral end of the head decidedly on the ventral side exactly as in Myxinoids. Since moreover the rostral end of the head must be formed by the ethmoidal region, there is strong reason to believe that *Palaeospondylus* is a form belonging to the same branch of the Ostracoderms as the *Heterostraci* and Myxinoids, though it seems to be more closely related to the latter than to the former.

The long paired strange skeletal piece (*p. nl*, text-fig. 102) which in *Palaeospondylus* is continuous with the otic region, and which lies in a level somewhat beneath the vertebral column, is, as is evident from several of the models made by SOLLAS, curved somewhat medially with the posterior end simultaneously as the medial side displays several irregularities and often is as a whole somewhat excavated. As there can be no doubt that this skeletal piece belongs to the endoskeleton, it seems in all respects to agree so well with the pronephros-lamella (*p. nl*, text-figs. 33—35, section series F, nos. 8—28) of the Cephalaspids that I feel sure of that it must be such a lamella; and it will therefore be referred to as pronephros lamella. It is, however, considerably longer and stronger than that in the Cephalaspids, a circumstance which indicates that the pronephros also must have been better developed and have played a much more important part than in the Cephalaspids. And we thus also find in this a Myxinoid-like character.

That the paired skeletal element of *Palaeospondylus* interpreted here as a pronephros lamella would have been a support for a pectoral fin and thus a shoulder-girdle, as has been maintained by certain writers, or that, as imagined by other writers, it would represent a vestigal part of a dorsal shield, is of course from what is known of it now quite excluded. It is also clear that the pronephros lamella cannot have formed a support for the branchial basket either, but that the branchial basket must have been short and have reached only slightly backwards beyond the posterior end of the otic region. Everything thus seems to indicate that the gills were situated in the main ventrally to the endocranium, as in the *Anaspida* and the *Osteostraci*, or as in the Myxinoid embryos (cf. text-fig. 101).

According to SOLLAS, there were several independent visceral elements ventrally to the endocranium. The figures given by SOLLAS, however, do not convince me that this really is the case. And until further evidence is put forward to the contrary, I feel inclined to see at least in certain of the structures interpreted by SOLLAS as visceral elements simply ridges on the the ventral side of the neurocranium, ridges corresponding to the interbranchial ridges of the Cephalaspids. And if this is true, we should have in this an additional support for the opinion that *Palaeospondylus* is closely allied to the Ostracoderms.

Finally it deserves to be pointed out in this connection that the orbital floor and certain lateral parts of the ethmoidal region perhaps are of a visceral origin and thus are comparable to the subocular arch in the Petromyzontids and Myxinoids.

As far as can be judged with our present knowledge of it, it seems fairly certain that *Palaeospondylus* is closely allied to the Ostracoderms and pertains to the same branch of these as the *Heterostraci* and thus to the branch that I have called above the *Pteraspidomorphi*. And since in certain respects it seems to be suggestive of the Myxinoid embryo, it is not inconceivable that it may reveal itself as a direct ancestor of the recent Myxinoids, or at least as an offshoot of the primitive Myxinoids[1].

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[1] The eel-shaped *Hypospondylus hohemicus* descriced by JAEKEL (1911) from the lower Carboniferous of Bohemia is too imperfectly known to be compared to the Ostracoderms, and its affinities with these cannot therefore at present be ascertained.

Arthrodira and Antiarchi.

From the account given above of the Ostracoderms it is fully evident that these cannot have had anything to do with the Arthrodires, which I have been able to show (STENSIÖ, 1925 b) are true fishes allied to the Elasmobranchs.

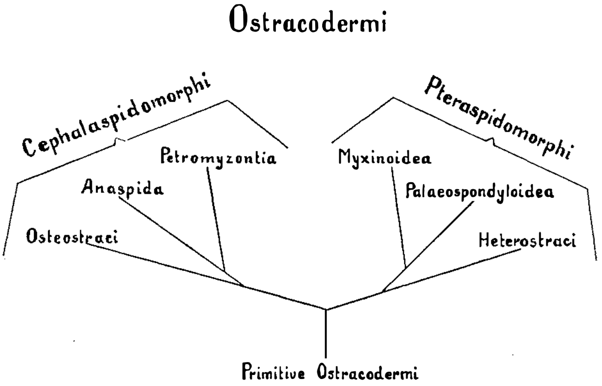
As the *Antiarchi*, according to studies carried out by the present writer on a larger material of *Bothriolepis canadensis*, are true gnathostomes allied to the Arthrodires, it is clear that they cannot any longer be referred to the Ostracoderms as has often been done hitherto.

Summary and Conclusions.

After having above dealt with the *Cephalaspidae* in detail, and after having compared them with the *Trematаspidae*, the *Anaspida*, the *Heterostraci*, the *Cyclostomata* and the *Arthrodira* and *Antiarchi*, I shall now briefly summarize here the most important results gained. These are as follows:

1. The *Ostracodermi* constitute a group of primarly agnathous craniate vertebrates, of an on the whole rather uniform organization, and have nothing to do either with the *Arthrodira* or the *Antiarchi*, which are true fishes related to Elasmobranchs.
2. The *Ostracodermi* comprise the *Osteostraci*, the *Anaspida*, the *Heterostraci*, *Palaeospondylus* and in addition — and this is very noteworthy — the recent *Petromyzontia* and *Myxinoidea*.
3. The *Ostracodermi* with this definition appear to consist of two different groups, one of which comprises the *Osteostraci*, the *Anaspida* and the *Petromyzontia*, while the other is made up of the *Heterostraci*, *Palaeospondylus* and the *Myxinoidea*.
4. And we thus find that the *Petromyzontia* and *Myxinoidea* are not merely related to the *Ostracodermi* but must be referred to these and pertain to different groups of these. Further it is clear that the *Petromyzontia* must have evolved either from the *Anaspida* or from the common ancestors of these and the *Osteostraci*, whereas the Myxinoidea are descendants either from *Palaeospondylus* or from primitive *Heterostraci*.
5. The interrelationships of the *Ostracodermi* would, according to our present knowledge, be as shown in the accompanying diagram.

   For the group comprising the *Osteostraci*, *Anaspida* and *Petromyzontia* I have chosen the name *Cephalaspidomorphi*, for the other group, consisting of the *Heterostraci*, *Palaeospondyloidea*



Text-fig. 103. Diagram showing the interrelationships of the *Ostracodermi.*

(*Palaeospondylus*) and the *Myxinoidea* on the other hand, the term *Pteraspidomorphi* has been suggested.

6. If we would try to express what is known so far of the interrelationships of the *Ostracodermi* in a classification it would be as follows:

VERTEBRATA CRANIATA

Branch I **Agnathi**
Class **OSTRACODERMI** (*Cyclostomata*)[1]
Subclass A **Pteraspidomorphi**
  Order 1. *Heterostraci*
  Order 2. *Palaeospondyloidea*
  Order 3. *Myxinoidea*
Subclass B **Cephalaspidomorphi**
  Order 1. *Osteostraci*
  Order 2. *Anaspida*
  Order 3. *Petromyzontia*
Branch II **Gnathostomi**

In the subclass *Pteraspidomorphi* the rostral part of the head is formed by the ethmoidal region of the cranium, and the nasohypophysial opening lies on the ventral side of the head, more or less close in front of the mouth. In the subclass *Cephalaspido-*

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[1] As having the priority the name Cyclostomata should, if we wish to be correct, replace *Ostracodermi.*

morphi, on the contrary, the rostral part of the head is formed by the excessively developed upper lip and is thus of a visceral origin; and moreover as a consequence of the strong development of the upper lip the naso-hypophysial opening lies in them on the dorsal side of the head, far behind the rostral end of that.

7. The presence of bone both in the exoskeleton and in the endoskeleton of the earliest appearing *Ostracodermi* is a highly interesting fact which shows that bone is a tissue which must have arisen very early, even in the most primitive agnathous vertebrates and certainly already in the ancestors of the Ostracoderms. And as this is the case, there is strong reason to believe that bone was present also in the ancestors of all the Gnathostomes and that the Gnathostomes all primarily had a more or less bony skeleton. Accordingly we have here an additional support for the opinion advanced by the present author in an earlier work (STENSIÖ 1925 b, pp. 160—164, 187—189) that the Elasmobranchs primarily had a bony skeleton.
8. Since a well developed bony endoskeleton is found in so primitive forms as the *Osteostraci* it seems not improbable that the exoskeleton did not give rise to the endoskeleton, as has been generally maintained, but that both were simultaneous formations. This is also in accordance with the fact that a well developed bony endoskeleton is found in most early fossil groups of fishes. And it is also more easy to understand that the connective tissue as whole acquaired the power of ossification than that it primarily had this power only in certain limited external parts.
9. In most of the fossil Ostracoderms there was a shoulder-girdle and more or less well developed pectoral fins.
10. The *Petromyzontia* and *Myxinoidea*, as being persistent representatives of the *Ostracodermi*, must be primitively lowly organized agnathous craniate vertebrates and not degenerated fishes. But it is quite clear that with regard to the skeleton they have undergone a regressive development and that the absence of paired fins, at least so far as the pectoral fins are concerned, is secondary in them.
11. Finally, it is clear now that the *Ostracodermi*,though very lowly organized, are true craniate vertebrates which have nothing whatever to do either with the *Arthropoda* or with the *Annelida*.

The investigations carried out in this work have thus thrown light not only on the organization of the *Cephalaspidae* but also on the *Ostracodermi* as a whole; and we have even been able to establish that the Ostracoderms still persist in the recent *Petromyzontia* and *Myxinoidea*, though they play a much less important part than during the early palaeozoic time.

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