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## A Consideration of Ostracoderms

D. M. S. Watson

*Phil. Trans. R. Soc. Lond. B* 1954 **238**, 1-25  
doi: 10.1098/rstb.1954.0004

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## A CONSIDERATION OF OSTRACODERMS

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(Received 26 January 1954)

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A survey of the great mass of papers which have appeared since 1920 dealing with the ostracoderms shows that many matters of structure and interpretation are still in doubt, despite the existence of many exquisitely preserved fossils of members of the group, and detailed descriptions of them. Critical consideration of published accounts and of new materials show:

That Stensiö's account of the structure of the head skeleton of *Cephalaspis* is correct.

That the gills of *Cephalaspis* were more probably pouches of adult cyclostome pattern than of the type suggested by Stensiö.

That the series of gill pouches includes two (one innervated by the profundus and one by the trigeminus) anterior to the hyoidean or spiracular gill cleft.

The heterostracan *Anglaspis* appears to have had gill pouches, and shows nasal openings lying on the roof of the mouth cavity.

The joint naso-hypophysial opening of cyclostomes on the top of the head is formed, as Goodrich showed, by the development of an upper lip as part of a larval feeding mechanism, so that cephalaspids, anaspids, lampreys and hagfishes are brigaded together with the probability that in their ancestry there were animals with an ammocoete larva.

The cephalaspid pectoral fins are shown to be neomorphs, not homologous with those of craniates.

The so-called 'electric fields' of *Cephalaspis* are newly interpreted as special sense organs allowing pressure waves incident on the head to be conveyed along liquid-filled canals to the ear.

The character of the body cavity of *Cephalaspis* is such that it is probable that its heart already showed a characteristic cyclostome asymmetry.

## SURVEY OF PREVIOUS WORK

The first fossils ever found in the Old Red Sandstone of England were bony (or apparently bony) plates which, by analogy with living animals whose anterior ends were covered with similar structures, were believed to be fish.

The first satisfactory account of these remains was given by E. Ray Lankester (1868) who divided them into two groups, the Heterostraci in which true bone was absent, and the Osteostraci in which it is always to be found. Lankester states that the only reason for associating these two groups with one another is that the creatures are craniate with the anterior ends covered by large plates, and are found together! None the less, Cope (1889) brigaded the two together as ostracoderms.

In 1899 Traquair described a magnificent craniate fauna of (?) Downtonian age from rocks near Lesmahagow in Lanarkshire, Scotland. This included an obvious but primitive osteostracan called *Ateleaspis*, and representatives of two essentially new groups. One, the anaspids, contained two genera of fish-like vertebrates, *Birkenia* and *Lasanius*, characterized by having a series of close-packed circular gill openings in an oblique line well behind the eyes, and a laterally compressed body with a caudal and one median fin, but no paired fins whatever. The other essentially new group, the Coelolepida, contained fish-like animals with a dorso-ventrally depressed and widened anterior end, and a narrow body with a median, and a forked caudal fin. These animals have a coating of 'placoid'-like scales which may be merely denticles, and no other hard parts. Two genera, *Thelodus* and *Lanarkia*, were recognized by Traquair, who adopted the former generic name from Agassiz who had used it for isolated scales from the Ludlow Bone bed. The posterior corners of the enlarged 'head' of these creatures protrude outward and were compared by Traquair with pectoral fins, there being no trace of any pelvics.

Thus by 1900 we had a considerable knowledge of the external structure and histology of these craniates commonly included in the Ostracodermi. But we had no real basis for an understanding of their relationships and systematic position. In 1924, J. Kiaer described a series of new anaspid genera from Ringerike in Norway which were much better preserved than those on which Traquair had founded the group. Kiaer showed that the dorsal surface of the head of these animals, in the area lying between the eyes, was perforated by two holes, each surrounded by scales fitted into the general external coating of the animal. The posterior of these holes, small and circular, was evidently for the pineal; the anterior, with paired expansions behind and a median extension forward, can be compared only with a similar opening in the osteostracan *Auchenaspis*, and with the naso-hypophysial opening in lampreys. From this point Kiaer proceeded to show that the row of gill openings on each side of the animal passes downward towards the ventral surface and inward toward its fellow as it is followed backward, and thus in all respects resembles those of lampreys. Finally, he pointed out that Traquair had reversed the dorsal and ventral surfaces of his fish, and that the caudal fin was not a heterocercal type, like that of elasmobranchs, but was reversed, the muscular end of the body passing into the lower lobe of a forked tail. This condition is found in modern animals (and then in a rather indefinite manner) only in the Ammocoete larva and even in the adult stage of *Petromyzon*. Thus

Kiaer claimed that the anaspids were cyclostomes, and that the cephalaspids were also members of that group.

*E. A. Stensiö's models of Cephalaspis*

The next important work was by Stensiö (1927) on the structure of *Cephalaspis* and its allies. He examined the structure of the head, not only by ordinary preparation, but by Sollas's method of grinding sections, recording their structure, and then grinding a determined distance farther, drawing again, and ultimately making a wax-plate model in the ordinary way. Thus Stensiö made a series of enormously enlarged models, which display all the bony structure of the head with great perfection, and he offered an interpretation in the greatest detail of the structures so discovered which is perfectly self-consistent and convincing. Stensiö's interpretation has never been successfully attacked and is clearly valid, but it seems possible to go further in its understanding, for his paper is immensely detailed, and somewhat difficult to understand because it provides no semi-diagrammatic drawings as a key. Figures 1, 2 and 3 of the present paper are such, drawn with great care from Stensiö's illustrations of his models, controlled at all points by reference to the published series of drawings of ground sections of *Cephalaspis hoeli*.

*Their brain, cranial nerves and ear show close parallel to Petromyzon*

From these sections and models Stensiö was able to show that the head of *Cephalaspis* was largely occupied by a material, presumably cartilage, which had definite limits, as is shown by the fact that all its surfaces (including those of the canals which conveyed blood vessels and nerves passing through it) may be covered by an extremely thin continuous film of bone, which in the fossils preserves its shape to perfection. This mass of cartilage is continuous with the brain case, and the shape of the cavity within which the brain lay is perfectly preserved. This 'brain cavity' can be filled easily and perfectly by fitting into it the brain, olfactory organ and 'hypophysis' of a lamprey. When this is done, foramina leading into long tubes of bone which pass through the head cartilage of *Cephalaspis* can easily be identified by comparison with *Petromyzon*, and can be accounted for completely by a series of cranial nerves and blood vessels of the same nature as those in lampreys. These structures taken together are of such complexity that it is impossible not to believe that Stensiö's restoration is correct in essence; even the minute IVth cranial nerve has its own independent canal. The cavity which contained the membranous labyrinth of the ear shows most clearly the presence of an anterior and a posterior semicircular canal, and the absence of any horizontal canal, as in lampreys. The close resemblance of *Cephalaspis* to the lampreys was thus placed beyond doubt by Stensiö, but there still remain various matters which demand further consideration.

STRUCTURE OF *CEPHALASPIS*

*Shape in relation to feeding habits*

The very complete, though superficial, ossification of these cartilages of the head of *Cephalaspis* makes it possible to discuss many features of the 'soft anatomy' of that animal. *Cephalaspis* was an aquatic animal adapted to a life spent on the floor of a lake; its ventral surface is thus accurately flat, the head being greatly widened so that there is a sudden



reduction of width at the anterior end of the trunk. From the transverse faces which thus lie on each side of the anterior end of the trunk a pair of movable flaps project directly backward. The trunk is rather accurately triangular in cross-section, but its lateral edges are rounded off as it passes into the back of the head so that the lateral parts of the head shield are shallow, their dorsal surfaces passing by rounded grooves into the central region. It seems therefore obvious that the animal fed on the surface of the lake floor, a region which is commonly very rich in potential food: organic detritus, small animals which eat it, bacteria causing its decay, and probably algae using manurial salts set free by the bacterial attack.

*Structure of head shield, mouth and branchial cavity*

The whole dorsal and peripheral parts of the head shield are composed of a superficial sheet of bone of most complicated shape, continuous throughout, and sometimes continuous from side to side under the anterior end of the trunk, or even sheathing that part of the body for some distance. The whole structure is evidently rigid despite the fact that a large circular area of the ventral surface is occupied by a flexible skin containing, variably, small plates or very small and numerous scales. Thus, with the marked exception of the mid-ventral area, the whole head of *Cephalaspis* is an extraordinarily rigid structure. Its volume is thus fixed unusually completely, an arrangement which produces certain functional difficulties.

In *Tremataspis*, an early cephalaspid, there is a point projecting backward from the middle of the lip (the anterior part of the border of the ventral flexible area), whose sides seem to be worn by contact with a pair of bony plates in the flexible region, and the members of this pair seem to have worn against one another—if a demonstration Professor Patten gave me on 23 September 1932 in London\* is to be believed. A. Heintz has shown that in *Aceraspis* the mouth lies immediately behind the rim of the head shield where there is a tooth-covered area well seen in many cephalaspids. In *Didymaspis*, for example, a definite triangular area passes backward and upward from this lip, is beset with small denticles, and can only have formed the roof of the 'mouth'. Indeed, in a specimen from my collection (D.M.S.W., P. 499) there is a series of small, ogival pointed teeth at the margin. This area, part of the suprabranchial plate, is bounded by two ridges along which Stensiö found that the anterior ends of the dorsal aorta lay in special grooves. He showed also that in many forms this area has a special, forwardly directed venous drainage. But in *Aceraspis* this mouth lies at the anterior end of a large area of the ventral surface where the small regularly arranged scales which cover it die out. In *Micraspis* the mouth seems to have moved backward, so that there is a crescent-shaped flexible strip of ventral surface separating the mouth from the backwardly turned rim of the head shield. Thus the nature of the mouth varies somewhat, presumably in association with particular feeding habits.

Stensiö showed that this supra-oral area is part of the great suprabranchial plate, which anteriorly is, throughout its whole extent, continuous with the deeper surface of the dermal head shield and the brain case, and is thus so much stiffened as to be inflexible. The low, transversely directed ridges, which separate shallow depressions on its ventral surface, are grooved for epibranchial arteries passing inward to the aorta, and are evidently the place

\* *Science*, 19 June 1931, **73**, 673.

of origin of some structures which separate loculi in which the gills lay. Farther back the median groove for the dorsal aorta is floored by bone and becomes a tube, passing through the suprabranchial plate to continue below the vertebral column. At the point where it is penetrated by the dorsal aorta the suprabranchial plate becomes free of the brain case, and passes outward and backward as an inverted bowl-shaped structure, whose borders rest upon the deep surface of the flat ventral part of the head shield round the central opening. The lower surface of this concave plate is drawn out into bony ridges, of considerable and sometimes great projection, which swing round so that they run almost radially. These are in series with the low ridges in the anterior region and evidently separated one gill space from its neighbours. Their depth must have greatly stiffened the unsupported posterior sheet of the suprabranchial plate, which is a thin cartilage with paper-thin bone covering its two free surfaces. Each of the grooves mapped out by these ridges leads down to a notch in the border of the flexible area in the ventral surface of the head shield, and, as shown most clearly in *Tremataspis*, each of the notches is converted into a circular pore by the plating or scaling of the area within. Each groove shows evidence of the existence of an epibranchial artery leading into the dorsal aorta, either directly in the anterior region, or through a collecting vessel for the posterior gills. And each groove is supplied by a cranial nerve, which splits into an anterior and a posterior branch in the region where it emerges from the suprabranchial roof.

*Probable nature of gills*

Thus each groove contained a gill, whose nature has to be considered. It seems quite incredible that these gills could ever have been those of true fish. There is no place where a branchial arch skeleton could be accommodated within the substance of the known structures, and it seems inconceivable that any such skeleton could be included within the space surrounded by the known skeletal structures which lie so much more superficially. Thus, as Stensiö showed, the gills are more likely to have been similar to those of cyclostomes. But there are two kinds of cyclostome gill: that common to adult lampreys and myxinoids, and that found in the larval ammocoete. Stensiö in his well-known reconstruction (1927, p. 161, fig. 37) restores *Cephalaspis* after the latter pattern.

The evidence on which we can judge in this matter is slender but seems to me to lead to another conclusion. *Cephalaspis* may be a large animal, with a head shield 30 cm across so that it presumably needed to pass a large volume of water over its gills. Thus it is most improbable that a ciliary stream would be adequate, and we must envisage a pump driven by muscles. The existence in every known individual cephalaspid of a flexible membrane within the area mapped out by the external gill openings suggests that the floor to the branchial region so formed was raised by muscles, water expelled through the gill pores preventing the formation of a 'virtual vacuum' below the head, as a similar disposition does in skates and rays. If we assume (for at present we have no direct evidence on the matter) that a flexible unossified cartilage extension of the suprabranchial plates passed across the intrabranchial region of the ventral surface, it is easy to restore a simple musculature passing from the dorsal intrabranchial ridges to their ventral continuations. This by contracting would reduce the volume of the pharynx and expel respiratory water, which would be replaced when the flexible floor returned to its original place by an elastic





## A CONSIDERATION OF OSTRACODERMS

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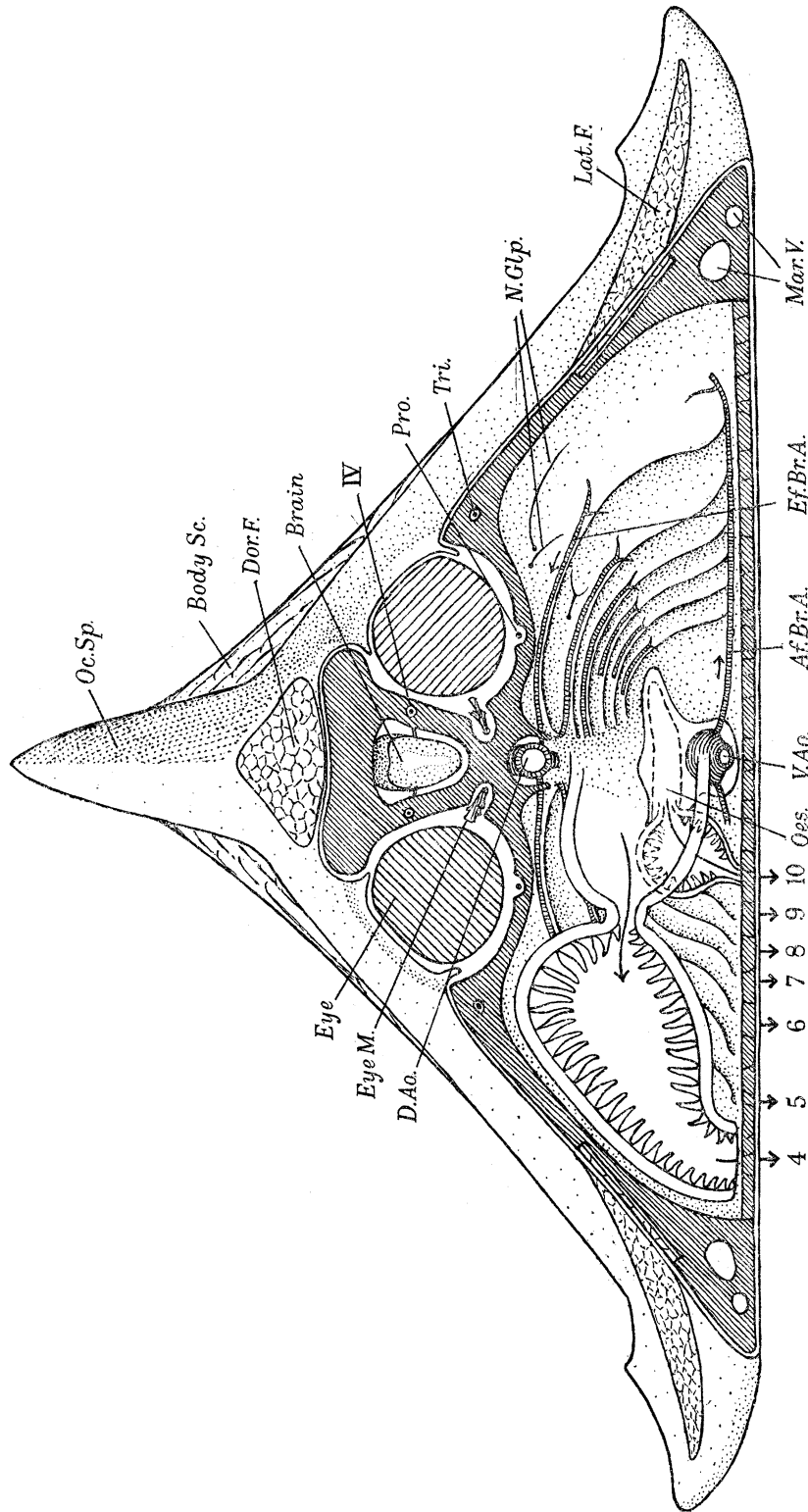


FIGURE 2. *Cephalaspis hoeli*. (Magn.  $\times 12$ .) The head is cut across through the fourth gill pouch and viewed from in front. The oesophagus, and gill pouches nos. 4 and 10 have been restored on the animal's right side. *Af.Br.A.* afferent branchial artery; *Body Sc.* body scales; *D.Ao.* dorsal aorta; *Dor.F.* dorsal field; *Ef.Br.A.* efferent branchial artery; *Eye M.* eye muscle (recte); *Lat.F.* lateral field; *Mar.V.* marginal vein; *N.Glp.* glossopharyngeal nerve; *Oc.Sp.* occipital spine; *Oes.* oesophagus; *Pro.* profundus nerve; *Tri.* trigeminal nerve; *V.Ao.* ventral aorta; *IV*, *IV*th cranial nerve.



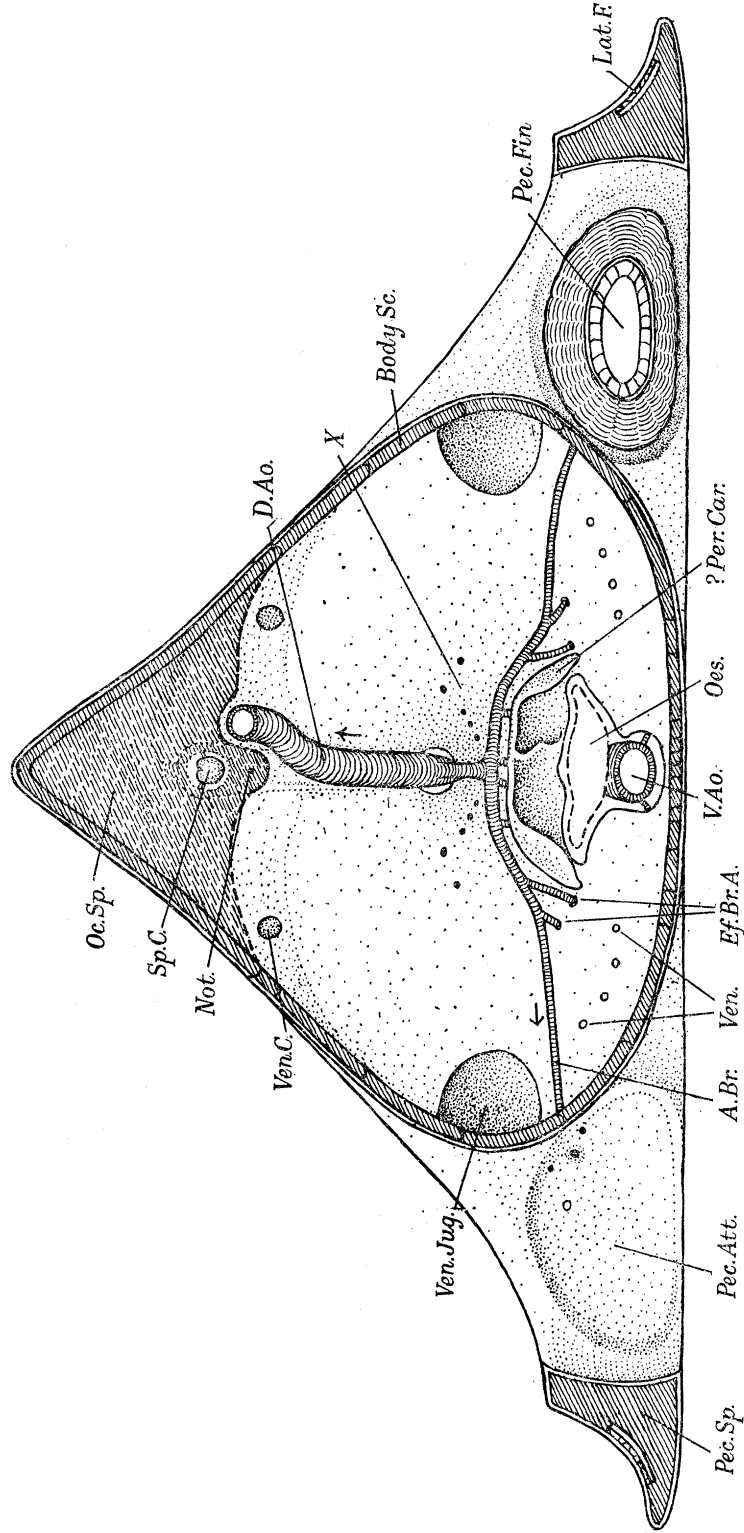


FIGURE 3. *Cephalaspis hoeli*. (Magn.  $\times 12$ .) Cut across the body, about at the third spinal nerve, and viewed from behind. The pectoral fin, cut across on the right, is removed on the left side, and is surrounded by the external surface of the pectoral sinus. *A.Br.* artery to pectoral fin; *Body.Sc.* body scales cut across; *D.Ao.* dorsal aorta; *Ef.Br.A.* efferent branchial arteries; *Lat.F.* lateral fin; *Not.* notochord; *Oc.Sp.* occipital spine; *Oes.* oesophagus; *Pec.Att.* facet for pectoral fin; *Pec.Fin.* pectoral fin; *Pec.Sp.* pectoral spine; *?Per.Car.* bony processes perhaps related to the pericardium; *Sp.C.* spinal cord; *V.Ao.* ventral aorta; *Ven.* venous foramina; *Ven.C.* vena capitis lateralis; *Ven.Jug.* vena jugularis; *X*, branches of Xth nerve.

recoil, perhaps aided by the contraction of a muscular sheet crossing it transversely. Simple calculations show that, in muscles passing directly from dorsal to ventral attachments in such a pharyngeal skeleton, even a reduction by one-fifth of their extended length would produce in the region as a whole volume alterations sufficiently great to change the water lying in any reasonable gill completely (or nearly so) at each contraction. Such an arrangement is entirely consistent with the universal retention of a flexible intrabranchial region on the ventral side of the head of animals which exhibit extreme rigidity in all the rest of that region.

The actual nature of the gills should now be discussed: that they were not similar to those of fish needs no demonstration. They could presumably have been either ammocoete or adult cyclostome gills. The difference between the two is essentially that the adult gill is a subspherical pouch with a definite wall, separated from its surroundings by a liquid-filled space, opening to the pharynx and to the exterior through tubes of circular section, small in diameter when compared with the pouch. In the ammocoete gill the wall of the chamber is firmly attached to the branchial skeleton and its musculature so that it cannot be freed from it easily by dissection, and it opens widely and directly into the pharynx. It seems most probable that the adult type best fills the available space in the *Cephalaspis* head, and that it was connected to the external gill opening by a definite tube, which arose from the lateral end of each gill pouch, passing outward and then turning suddenly backward and downward so that the impression it makes on the suprabranchial plate is (in *Kiaeraspis*) markedly distinct from that of the pouch, being moulded over a 'knee' in the duct (cf. Stensiö 1927, fig. 36, p. 158).

#### CONSIDERATION OF GILLS IN OTHER OSTRACODERMS

Thus there is evidence suggesting that *Cephalaspis* possessed gills of adult cyclostome pattern, and it is interesting to consider whether such gills existed in other ostracoderms. The earlier members of the Heterostraci, of Downtonian age, have long been known (Woodward, 1891, p. xvii) to show some evidence of the structure of the gills, and this evidence must now be considered. It is best presented by Wills (1935) for the English Downtonian *Anglaspis*, building on a foundation laid by J. Kiaer (1932*a*, as edited by A. Heintz) from Spitzbergen material.

#### STRUCTURE OF *ANGLASPIS*

##### *Head armour*

The skeleton of the anterior end of the body of animals of this genus consists of a dorsal shield, which is a sheet of calcified material, not extending into the endocranium, but of dermal origin, which coats the dorsal and the upper part of the lateral surfaces from its extreme anterior end backward to the hinder end of the gill region, turning downward over the anterior end to form the upper border of the just not terminal mouth. Laterally the lower border of this shield is notched for the upper halves of the very small orbits, and more posteriorly by a wide excavation, which has a special surface sculpture and is the upper half of the exhalant respiratory opening. The mouth lies immediately behind the backwardly rolled transverse border of the anterior end of this shield, and its angle is

marked by a suborbital plate, bearing the lower half of the orbital margin, which in front of the eye is scarfed on to the inner surface of the border of the dorsal shield, and posteriorly is attached to the branchial plate. This is a plate which encloses a deep groove of almost semi-cylindrical section and forms a very distinct outstanding ridge on the animal's flank from the eye backward. Its dorsal border seems to have been in continuous contact with the lateral border of the dorsal shield from the eye backward to the point where the large exhalant opening lies between the two 'bones', each of which is thickened so as to surround the opening with a bony ring with an unusual ornamentation of nearly parallel ridges. This widened patch of upper border is continued forward on the visceral surface of the lateral plate as the floor of a groove. The head armour is completed by a ventral shield which is attached to the lower border of the lateral plates and extends forward to end in a transverse margin, to which a series of oral hard parts was attached. The body seems to have passed directly into the posterior end of the armour so constructed, whose elements, if we may judge from the dorsal and ventral shields, were scarfed on to the anterior ends of the first ring of body scales by a facet conforming to the scale ornament. This ring of scales consists of a pair of enormous plates which must articulate with both dorsal and ventral shields, and with the branchials; in addition there are dorsal and ventral ridge scales and probably three other pairs of small scales. This structure of the anterior part of the body is found in all the members of the most primitive family, the Monaspidae; in the Cyathaspidae the dorsal shield is subdivided, but may be fused with the branchial; in the more advanced pteraspids there is further subdivision, but the branchial is commonly fused with the dorsal in old individuals. In no form has the ventral shield been found fused with the dorsal armour. None the less the overlap of both dorsal and ventral shields on to a single body scale on each side in *Anglaspis* and *Poraspis* makes it most unlikely that the two elements could in life have moved with respect to one another.

It therefore appears that the anterior part of the body of a heterostracan was effectively of fixed volume, though the subsequent development of such creatures as *Drepanaspis*, in which the large plates are separated from one another by small ones, may have allowed changes of body shape to have taken place.

#### *Branchial cavity and gills*

It seems evident that the gills of Heterostraci were pouches of adult cyclostome pattern, because only such structures could have made the impressions on the dorsal and ventral shields which are shown especially well in natural moulds of *Anglaspis* and *Poraspis*, and were first recognized by A. Smith Woodward in *Cyathaspis sturi* in 1891. In this material impressions on the dorsal shield obviously made by the pineal body and the vertical semi-circular canals of the ear fix definite points, and from a place lateral to the ear backward each gill pouch makes a shallow depression on the visceral surface of the dorsal and ventral shields, whilst the exhalant duct, at a point where it bends over to pass downward and backward, makes an independent impression, on the lateral part of the dorsal shield, which is obliquely placed, its lateral end being directed backward. Such impressions, to a total number of ten or eleven, succeed one another in *Anglaspis* on each side of the mid-line from a point almost exactly between the eyes backward. The exhalant opening between the dorsal and branchial plates lies at the level of the seventh gill pouch.

It is easy to draw transverse sections through the head region of *Anglaspis* which give the external form of the body and the markings on the visceral surfaces of the dermal plates, and two such sections are shown in figure 4. In such figures, as the minimum width across the ears is known, it is possible to draw a hypothetical brain case, and thus gain some idea of the size and general structure of the gills. Figure 4B is of a section passing immediately behind the ear through the fifth pair of gills. In it the brain case is given a width suggested by that of the semicircular canals, and some allowance is made for blood vessels, etc. The

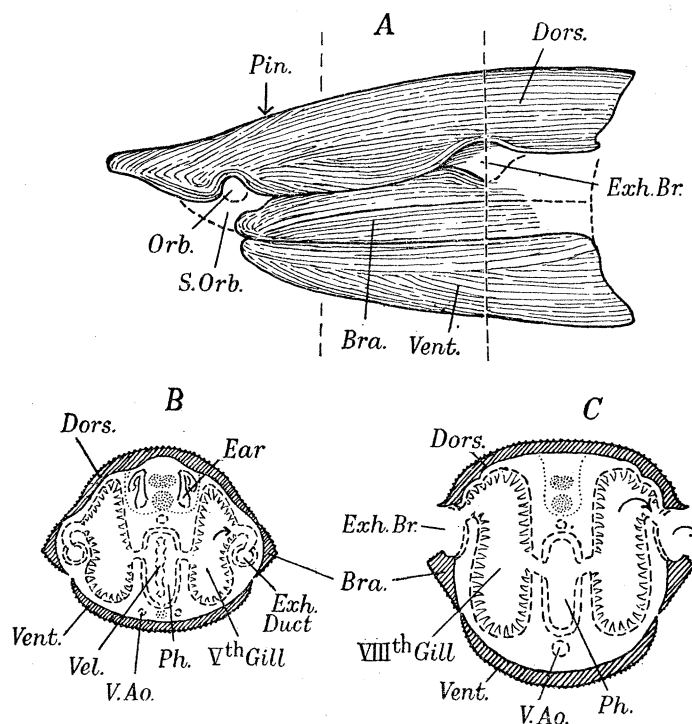


FIGURE 4. *Anglaspis macculoughi*, A.S.W. (Magn.  $\times 2\frac{1}{4}$ .) A, restoration of head shield, from the left side. B, transverse section at the anterior marked point in A. C, transverse section at the posterior marked point in A. Bra. branchial shield; Dors. dorsal shield; Exh.Br. common exhalant opening; Exh.Duct. common exhalant duct; Orb. orbit; Ph. pharynx; Pin. pineal; S.Orb. suborbital; V.Ao. ventral aorta; Vel. velum; Vent. ventral shield.

space available for each gill is much higher than it is wide and much shorter antero-posteriorly. The gill must almost necessarily open into the pharynx by a comparatively small opening, and must discharge through the branchial opening by a tube which was either a long independent duct, or a common duct, connected by a short tube to each gill in turn, running from some point immediately behind the eye to this opening. The lower surface of the hinder end of this common duct seems to have rested in a groove in the much widened upper border of the branchial plate.

#### Mechanism of gills

How this arrangement worked is not easily determined. The rigidity and apparent fixed volume of the anterior end of *Anglaspis* seems to make it impossible that inspiration and expiration were performed by movements of the pharyngeal region as a whole. The large size of such an animal as *Pteraspis dunni* makes it difficult to believe that ciliary currents



would be adequate. If the gill pouches were surrounded by large continuous blood spaces (Cole's 'blood lymph' peribranchial sinuses in *Myxine*) it would theoretically be possible to contract one pouch by muscular action, causing others to expand by sucking blood from the peribranchial space around them, and thus giving each pair of gills in turn a supply of new water. But such an arrangement seems impossible to associate with any reasonable rhythm of opening and closing the mouth, and with contraction of the heart. In fact it seems perhaps most probable that in *Anglaspis* the respiratory current was induced by movements of a large, muscular velum, as Cole (1907, p. 722) and Gustafson (1935) have shown to be the case in *Myxine*.

*Nostril and olfactory organ*

It is therefore necessary to consider the possible position of such a velum. It would naturally be formed from the remains of an oral plate, thus lying behind Rathke's pouch—the hypophysis—whose position on the roof of the head just in front of the eyes in adult cephalaspids and anaspids is clearly secondary. There is no trace of any such arrangement in any heterostracan. In all the members of that group there is no external sign of any nostril, and it has long been assumed that the olfactory organs opened into the mouth, but the only published evidence on the matter is a statement by Kiaer (published by Heintz) that the nostril so opens.

A specimen of *Anglaspis* (D.M.S.W., P. 762) which I prepared shows the arrangement clearly. Here the ventral border of the dorsal head shield from orbit to orbit is 'neatly finished' with two or three 'ornamental' ridges of the same nature as those which cover the external surface, running round it parallel to the border. These are cut off obliquely by the scarfed inner surface to which the anterior part of the suborbital plate was attached. Anteriorly this ventral rim bounds a plate lying above the cavity of the mouth which stretches across nearly from side to side of the anterior part of the head shield and ends behind at a transverse border a little anterior to the orbit. This plate is covered with small pointed denticles, which coalesce posteriorly into irregular sharp-edged transverse ridges; it thus forms the roof of the mouth, recalling though it is not homologous with, the supra-oral area of *Cephalaspis*. Laterally it is cut out by a rounded notch, clearly that of a nostril lying within the ventral border of the head shield. This nostril is roofed by bone, which is the lateral part of a definite depression on the under surface of the head shield which evidently housed the olfactory organs. The arrangement is singularly like that of a dipnoan. It is evident that the hypophysis opened behind this sheet of bone, but on the same surface as the nostrils. Thus the velum might well have been attached to the ventral surface of the brain case (whose nature is unknown) not far posterior to the hinder orbital margin. This point lies anterior to the first pair of gill pouches, and is thus possible.

*Stage of ammocoete development paralleled*

Heterostraci in general presumably agreed with *Anglaspis* in the nature and position of the nostril and olfactory organ which in them appears to have smelt, not food and other matters outside the mouth, but the actual contents of the buccal cavity. It is commonly believed that smell is primarily an exteroceptive sense of distant perception, as it is, for example, in a dogfish, or man, but the validity of this interpretation perhaps becomes

doubtful in view of the great age and primitive (?) nature of the Heterostraci. It is therefore important to realize that the relative positions of the two nostrils and the hypophysial opening on the same small surface is exactly that which occurs in the development of *Petromyzon*, as a condition prior to the development of the upper lip, and the pushing forward and upward of the three structures on to the top of the head, and thus antecedent to the development of the oral hood as part of a feeding mechanism functional through larval life as an ammocoete.

In the adult lamprey it is obvious from simple observation that the large hypophysial sac, separated from the cavity of the mouth only by an epithelium is compressed by each constriction of the pharynx and secures a regular supply of water to the olfactory sacs. But the existence of a continuous cartilaginous and bony floor below the hypophysis prevents this action in *Cephalaspis*, and makes it difficult to suggest a functional 'origin' for this structure. None the less it seems reasonable to interpret the head of *Cephalaspis* as originating in an ammocoete hood.

Stensiö (1932, p. 189), by an interpretation of von Kupfer's description of three developmental stages of the myxinoid *Bdellostoma*, has shown that the common naso-hypophysial opening and tube of these animals has arisen by the growth of a post-hypophysial upper lip as it does in *Petromyzon*, and as such a structure in the myxinoid seems to have no obvious function it is tempting to assume that the myxinoid ancestors had an ammocoete stage. Subsequently the gradual introduction of a large yolky egg enabled a larval period and metamorphosis to be suppressed.

This implies that the myxinoids, lampreys, cephalaspids and anaspids are to be grouped together by their common possession at an early evolutionary stage of an ammocoete larva. The Heterostraci, whose relationship to this group seems to be supported by the probable character of their gill pouches, form a different group which branched off before the introduction of the ammocoete, and their relations to the 'coelolepids' remain to be discussed.

#### STRUCTURE OF COELOLEPIDS

The only coelolepids of which anything beyond isolated scales is known are the very many specimens of *Thelodus* and *Lanarkia* from Lesmahagow, and those of '*Coelolepis luhai*' from Oësel. *Thelodus* and *Lanarkia* were well described by Traquair, and have been discussed by Stetson and Westoll; all that is preserved of them is an external coating of denticles in *Lanarkia*, and placoid-like scales in *Thelodus*. The animals are fish-like, with a wide and flattened anterior end, apparently always shown directly dorso-ventrally compressed, so that it is symmetrical, whilst the very much narrower body with a forked caudal fin and one median fin, either dorsal or ventral, is usually seen in side view, but may be obliquely crushed. The anterior border of the head is a wide transverse line, the two sides are nearly parallel anteriorly and then turn out a little to form flaps whose hinder borders pass straight in to the constricted body. The mouth is shown as a rounded opening surrounded by special small scales in *Lanarkia*, but is not shown in *Thelodus*. Dark patches may represent eyes placed where the anterior and lateral borders of the head meet. There are no traces of nostrils, pineal opening or gill openings. Traquair figured in *Lanarkia*, and Stetson (1928) has found in *Thelodus*, in single specimens, evidence of the existence of

paired series of structures which may well be gill pouches, like those which appear to have existed in *Anglaspis*. There is, therefore, practically no evidence to determine the relationships of these animals, but they might well be connected with the Heterostraci. In any case they are evidence of the general fin structure of craniates of their time, the most remarkable feature being that the 'pectoral fin' lies lateral to the last four gill pouches.

Another presumed coelolepid, the single specimen of *Thelodus* (*Cephalopterus*) *pagei*, has been interpreted by Westoll (1945) as a cephalaspid at a time of life before the consolidation of the head shield. Finally, '*Coelolepis luhai* Kiaer' from the Middle (?) Ludlow of Oësel evidently differs from other coelolepids, and Westoll has suggested that it is an anaspid. I have examined a large series of specimens (about one hundred) of this animal without gaining any clear evidence as to its affinities. The detailed preservation of the scales is perfect, but they are always somewhat misplaced, and the only visible structures are a small terminal mouth, with some enlarged scales round it, and orbits. There is no trace whatsoever of gill openings, nor, in those I examined, of fins. But one of the specimens described by Kiaer shows a hypocercal tail extremely similar to that of *Pteraspis*.

#### INTERPRETATION OF CEPHALASPID GILLS

It is therefore evident that the cephalaspids possessed cyclostome gills, usually ten pairs. The implication is that each of these opened out of the continuous and narrow, though deep, pharynx by a circular pore. The most anterior pair of gills lay largely lateral to the mouth cavity, and their internal cleft must have been only just behind it. Pouches 2 and 3 lie entirely anterior to the brain, 4 and 5 below the eye, and the remainder below the ear. In fact the whole series is uniquely far forward; even in an ammocoete the first gill pouch lies behind the infundibulum, in adults—whether lamprey or hagfish—it is more posteriorly placed. It seems evident that the condition in all cases is determined by functional needs. The immense anterior projection of the cephalaspis head shield, though it may be a derivative of an ammocoete hood, is part of the apparatus which enables the ventral surface of *Cephalaspis* to be flat, no doubt in association with the animal's apparently most successful feeding habits. And it is to this structure that the anterior position of the gills is due.

#### *Identity of head segments*

Stensiö showed that the first gill pouch was innervated by a profundus nerve whose roots perforate the cranial wall by two foramina, and whose distribution, shown by the bone-lined canals in which it lay, was more extensive, especially as it probably included a motor component, than that of any living craniate. Stensiö also showed that that distal part of this nerve which passes to the first gill pouch is identical in its nature with the corresponding parts of the trigeminus, facial, glossopharyngeal, and the six branchiomic portions of the vagus nerves.

Thus there was in *Cephalaspis* a complete series of gills, innervated in strict succession by all the branchiomic nerves from the profundus to vagus VI. Stensiö (1927, p. 166), discovering this condition, then goes on to say that these gills are from front to back: 'a pre-spiracular, a spiracular, and a hyoidean.' But, of course, a spiracular gill slit is actually a hyoidean gill slit, for the facial nerve forks over it, so that Stensiö thus applied what are actually morphologically identical names to two successive structures.

Thus seems to have arisen the common belief that Stensiö had shown the existence of *one* functional gill slit in front of the hyoidean segment when in fact he has established the presence of two, a first supplied by the profundus nerve, and a second by the trigeminus, the third being the hyoidean or spiracular. It follows, therefore, that *Cephalaspis* is unique, it has a more complete representation of all the segments of the craniate head than any other form, even in its embryonic stages.

#### COMPARISON WITH GILLS OF OTHER OSTRACODERMS

It is evident that in *Anglaspis* (and presumably in all other pteraspidomorphs) the gill series lies relatively much farther back than it does in cephalaspids. In *Anglaspis* the first gill impression lies very nearly between the eyes, and the third is lateral to the ampulla of the anterior vertical semicircular canal. It is not unreasonable to suppose (though there is no evidence available) that the first is a trigeminal pouch, the second a hyoidean or spiracular one. This would suggest that the profundus pouch was non-existent.

In anaspids the mouth is relatively greatly elongated, its corner in *Rhyncholepis* lying behind the orbit; in this form there is then a distance, greater than that from the snout to the back of the orbit, between the corner of the mouth and the first of the eight gill openings whose place in the cephalaspid series is thus impossible to determine. The elongated mouth is surrounded by large dermal bones, above and below, which suggest that *Rhyncholepis* caught relatively large prey, a habit consonant with its body shape and structure.

Anaspid gill openings are circular pores so closely set, especially in *Pharyngolepis*, that it is almost impossible to believe that the gill pouches from which they open did not extend farther along the body, a series of ducts of gradually decreasing length connecting them with their external openings, as they do in myxinoids. Such an arrangement must have a functional significance: in *Myxine* to allow the anterior end of the animal to be buried in its prey; in anaspids perhaps merely to accommodate an elaborate mouth musculature, acting on dermal bones and hence superficial to the gill pouches.

#### EMBRYOLOGICAL EVIDENCE

Thus *Cephalaspis* remains as the most primitive known craniate, but embryological evidence from craniates, first brought together by Balfour (1877), Marshall (1881) and J. W. van Wijhe (1882), shows beyond dispute that segmental mesoderm extends forward toward the front of the head, leaving an anterior mass (the region of a craniate head anterior to the hypophysis) undivided and without any nerve supply, unless perhaps the nervus terminalis. Segmentation in craniates is evidently primarily mesodermal, and its immediate function is apparently to provide a musculature which will allow an animal to swim by throwing the body into lateral waves propagated backward in succession.

#### PROBABLE ANCESTRY OF OSTRACODERMS

Thus *Cephalaspis* had in all probability ancestors of 'worm-like' shape, free-swimming, and with an 'ammocoete head' formed by a displacement forward and upward of the anterior unsegmented region, including the hypophysis, as a result of developing a micro-



feeding mechanism. And the anaspids are a parallel branch. But the Heterostraci, though of similar origin, branched off before the 'ammocoete' stage.

Comparison of cephalaspids and anaspids may thus be expected to throw some light on the nature of their common ancestor. Kiaer has discussed the body shape of the Norwegian anaspids, concluding that they had the form of active, free-swimming fish. *Lasanius*, with its well-developed series of postcephalic rods, affords definite evidence about body shape which has been discussed by Bulman (1930), and Simpson (1926). A very large specimen (D.M.S.W., P. 273, in which 17 dorsal scutes measure 64 mm. in length) shows the structure of the 'post-cephalic rods' better than any yet described, and in a somewhat different form, presumably resulting from greater age. The 'postcephalic rod' is one of a series of eight overlapping plates of 'bone' which extend along a ridge at the meeting of the lateral and ventral surfaces of *Lasanius*. Each plate is drawn out into a short backwardly directed lateral spine which lies horizontally and bears a horizontal ridge continued forward on to the body of the bone, so that the ventral part of the structure extends inward and forward from it. The dorsal part is a comparatively narrow rod, of oval section, extending upward and forward parallel to its fellows and to the row of gill pores. Each element is connected with its neighbour by a special forwardly directed process which lies in a groove in the next anterior element, and by a groove (which extends on to the admedian surface of the spine) with the articular process of the next posterior bone. As previous authors have pointed out there is a small systematic change in shape from front to back of the series of eight, but in all the 'rod' proper is directed upward and forward at about 45° to the animal's length, and the ventral part of the structure passes downward, inward and forward over the fish's ventral surface, its end being rounded.

I agree with Bulman's conclusion that the anterior part of the body of *Lasanius* was moderately flattened ventrally, but feel sure that the spines borne on the rods projected very little laterally, though they must have marked a ridge where the ventral passed into the lateral surface. The anterior rod seems to be spineless, differs somewhat in shape from its successor, and is no doubt the post-branchial plate of other anaspids. It seems evident that the whole 'rod', except probably the tip of its spine, lay in the skin, the elements agreeing in spacing with the myotomes on which they rested. But as each rod is a flat oval when cut across it seems probable that they were not entirely superficial and hence covered only by epidermis.

The post-branchial plate in *Birkenia* and the Norwegian forms wraps round the lower end of the row of gill pores and extends upward so as to support the branchial bones to which it had evidently a close attachment, and was important as providing the equivalent of a shoulder girdle to which the lateral body muscles could be attached.

It is evident that the 'post-cephalic rods' of *Lasanius* are not a pectoral fin, nor do they provide a starting point for development of such a structure, as there is no indication whatever that they were associated with ventral muscle buds from the myotomes.

#### *Structure of Tremataspis*

The earliest cephalaspids are those from the Middle Ludlow of Oësel, of which *Tremataspis* is by far the most abundant. Its structure is still badly known, though abundant material exists, and the only side view of the animal's anterior end is that by Patten (1903),

a posterior view of the head shield has never been published. Of the other forms we know even less, so that a serious discussion of the evolution of the group is impossible.

Several species of *Tremataspis* have been 'described', and there is evidence that *T. mammilata* differs from the *T. schmidti* described by Patten. I therefore give in figure 5 drawings made (without reconstruction) from a single specimen (D.M.S.W., P. 752). This specimen is cracked, slightly asymmetrical, but clearly essentially undistorted. The structures shown are entirely dermal, and must usually have been closely coated by the epidermis. It is to be

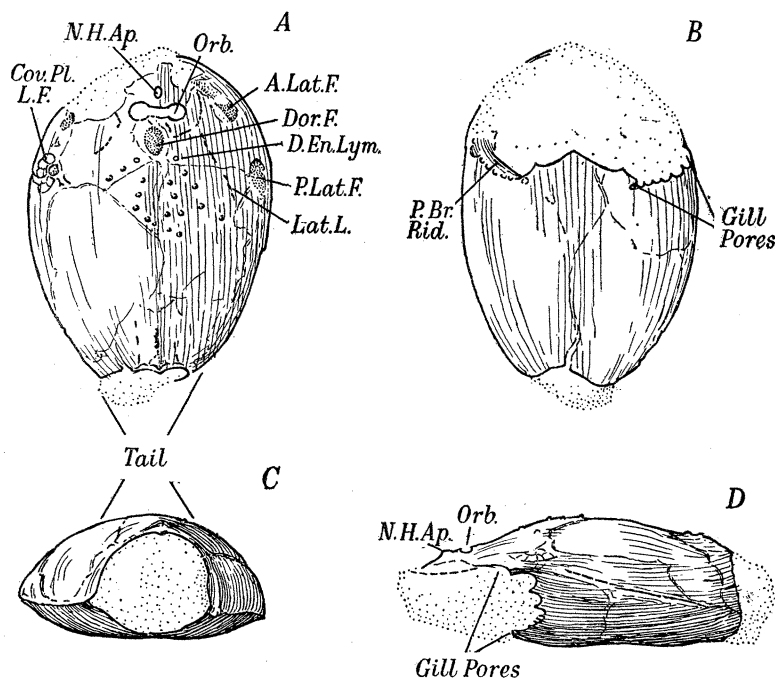


FIGURE 5. *Tremataspis mammilata* Patten. Head and body shield (D.M.S.W., P. 752). (Magn.  $\times 1\frac{1}{3}$ .) A, dorsal, B, ventral, C, posterior, D, left lateral aspect. In some large areas the dermal shield is stripped off leaving a clear impression on the matrix, the broken border is represented by a thin line. A.Lat.F. anterior lateral field; Cov.Pl.L.F. cover plate of posterior lateral field; D.En.Lym. ductus endo-lymphaticus; Dor.F. dorsal field; Lat.L. lateral line; N.H.Ap. naso-hypophysial aperture; Orb. orbit; P.Lat.F. posterior lateral field; P.Br.Rid. post-branchial ridge.

noted that the head and body armour are continuous, without any indication of where one passes into the other. The posterior opening to which the hinder part of the body was attached—its most anterior scales being overlapped by the anterior armour—is triangular, the rounded ventral surface being marked off from the rounded lateral surfaces by low ridges. The mid-dorsal line is a ridge, but the body here is as high as it is wide. From this point forward the body deepens a little and widens much, but its ventral surface is convex and there are lateral ridges continuous with those on the tail which rise as they pass forward to join the angles of the head shield above the gill openings. The gill openings form a paired series, the most posterior passing through the ventral shield, the others notching the border of the subbranchial opening, each lateral to that which lies behind it. Each pore lay in a notch in the head shield, the last seven forming an almost straight row outward, forward and upward. Their openings are strengthened by a deep flange of dermal bone, rising within the body cavity for a height of from 1 to 2 mm, which has a smooth

upper surface of considerable width and is entirely continuous with the ventral part of the head armour, its upper and outer end, less well ossified, being connected with it by slender strands of bone. I see in this ridge—which Robertson called the post-branchial ridge—a homologue of the post-branchial plate of anaspids, which has gained its actual position with the widening of the anterior end of the animal to achieve the ‘tadpole’ shape of *Tremataspis*.

#### *Significance of fins*

It is, I think, generally believed that craniates were originally marine, as are all protochordates—living and extinct. They must therefore have reached those streams and lakes, in whose deposits nearly all early craniate fossils have been found, by swimming up rivers. Swimming by lateral body flexure is the purpose of segmentation, and median fins at the hinder end of the body much improve the action. But other fins, although they increase stability in direct locomotion and are of great importance in determining course, are not necessary; after all, the sea lamprey regularly migrates from the sea to rivers to spawn, it can be caught at Worcester, some 50 miles from the sea.

Thus there is no reason to suppose that craniates possessed paired fins when they entered rivers and lakes. It is therefore reasonable to assume that the lack of paired fins in *Tremataspis* and anaspids is primary. A hypocercal caudal fin tends by its action to raise the head and is appropriate to free-swimming fish, the heterocercal fin depresses the head and is appropriate to a bottom-living form. Thus the fact that cephalaspids have a heterocercal, anaspids a hypocercal caudal fin is reasonable, and suggests that their common ancestor was indifferent in the matter, its tail being symmetrical.

*Tremataspis* shows to a different degree in its various species the development of lateral ridges, and a flattening of the anterior part of the body, the ridge rising as it passes forward over the gill region, so that lateral strips of the ventral surface slope downward and give a lift to the head of the forwardly moving fish necessary to balance the action of the tail and allow the animal to keep a level course. This lateral ridge, which meets the series of gill pores at about the seventh from the back and continues forward over the anterior openings, very evidently lies on a different plane from the lateral ridge made by the post-cephalic spines of *Lasanius*, the two structures having arisen separately.

A very striking quality of *Tremataspis*, which has never been referred to in print, is the oblique position of the ventral surface between the gill pores and its side to side curvature. In all Downtonian and later cephalaspids—*Cephalaspis*, *Hemicyclaspis*, *Benneviaspis*, *Kiaeraspis*, *Auchenaspis*, *Didymaspis*, to list only well described animals in which the facts are known—the ventral surface of the head, including the subbranchial space, is flat and lies parallel to the long axis of the fish (cf. Stensiö, 1932, pl. 3, fig. 1). It is, indeed, directly continued by the flat ventral surface of the anterior part of the flexible body in such a way as to show that the fish was in contact over a large area with a lake floor and had its mouth in immediate apposition to it. It is evident that this is a condition very different from that in *Tremataspis*, and one which obviously arose adaptively. One effect of its occurrence is that those oblique lateral parts of the lower surface of the head shield, which in *Tremataspis* keep the head up when the animal moves forward, have lost this function, and it seems certain that a *Cephalaspis* not provided with some alternative would drive its anterior end into the soil when the action of the tail drove it forward. Thus the ‘pectoral fins’ discovered

by Lankester have an obvious and necessary function, and their occurrence, so far as known, only in forms of ostracoderms with a flat ventral surface, is explained.\*

#### *Pectoral fin*

Heintz (1939, p. 100) draws a series of forms (whose relative ages cannot be determined by independent evidence) to show how the 'pectoral fin' could have arisen in cephalaspids by the development, in a form with a flat ventral surface, of flexibility in the postero-lateral region of the head, its gradual lengthening and detachment mesially, and finally its protection by the development of a spine lateral to it. The series seems completely convincing,

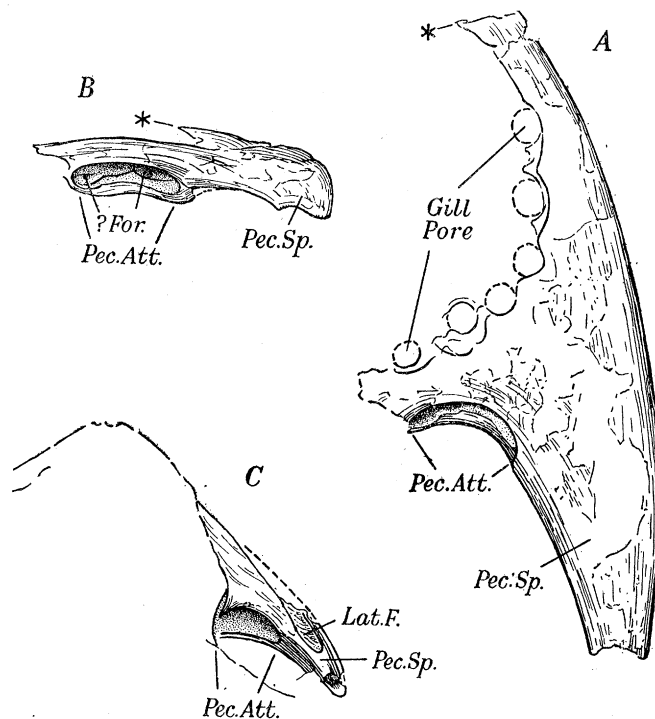


FIGURE 6. *Cephalaspis* sp. A (D.M.S.W., P. 367), ventral view of the left half of a head shield showing the branchial openings, 'pectoral sinus' and articular facet of the fin. B, same specimen, ventral surface upward, viewed directly from behind. C (D.M.S.W., P. 776), posterior view of the right side of a head shield to show the articular area for the pectoral fin. (Magn.  $\times 1\frac{1}{3}$ .) ? For. apparent foramina in the ossified cartilage of the attachment area for the pectoral fin; Gill pore, external opening of a gill pouch; Lat.F. lateral field; Pec.Att. attachment area on the ossified cartilage of the 'shoulder girdle'; Pec.Sp. pectoral spine.

and implies that the ancestral osteostracan was without paired fins. That this was the case seems certain; the Heterostraci, which lived alongside the cephalaspids, apparently pursuing a similar mode of life, never possessed such fins, unless perhaps the posterior 'corners' of the head of *Drepanaspis* and *Psammosteus* be so regarded. The plate which forms the 'corner' is often so worn as to suggest that it dug into the sand of the floor of the lake in which the animal lived, but there is no reason to suppose it was movable on the head shield. *Thelodus* and *Lanarkia*, coelolepids, have projections at the back of the head lateral to the hinder gills very much like those of *Ateleaspis*, the first term of the Heintz series, and

\* Denison (1951) suggests that the Middle Ludlow *Witaspis* and *Procephalaspis* from Oësel may have possessed pectoral fins; it is unfortunate that we know nothing of the existence of a 'shoulder girdle' in them, nor of their shape.



their tails may be heterocercal, there being no evidence on that matter. And it is safe to regard the pectoral fin of *Cephalaspis*, which lies laterally to gill pouches, as not homologous with that of gnathostomes.

The primary shoulder girdle of *Cephalaspis* is known only from Stensiö's account founded on a model (made from section of *Cephalaspis hoeli*) where it forms a shallowly concave surface, perforated by a series of foramina shown to have transmitted dorsal and ventral nerves, an artery and a vein draining into the marginal vein. I have developed the posterior surface of this shoulder girdle in *Cephalaspis* spp. (D.M.S.W., P. 367 and P. 776) (figure 6) which agree in showing that the ossified articular surface of the cartilage is deeply recessed, the dermal bone of the head shield turning over the edge and extending forward for some distance. In neither specimen is there any trace of an articulation for endoskeletal elements in the fin, though some of the foramina described by Stensiö are recognizable. In *Benneviaspis* sp. (D.M.S.W., P. 278) the endoskeletal girdle is unossified, but the opening in the exoskeleton leading to it exists.

It is evident that there is no such evidence, as Stensiö has shown to exist in many arthrodeirs, of a series of nerve foramina, passing through the shoulder girdle to supply a true pectoral fin formed from many somites.

#### REINTERPRETATION OF 'ELECTRIC FIELDS'

Westoll has emphasized that the fragmentary nature of the lateral-line system of cephalaspids contrasts very markedly with the great development of that set of sense organs in the Heterostraci, which lived side by side with cephalaspids. He went on to suggest that the so-called electric fields of cephalaspids represent some modification of the lateralis system. It is therefore interesting to discuss the possible function of these. The lateral field\* in *Benneviaspis*, for instance, whose skull is of the order of 60 mm wide, is a strip following rather accurately the outer border of the head and measures some 30 mm in length, 4 or 5 mm in width. As seen from the outside in an ordinary specimen it is a depression, the visible external surface dropping suddenly for a depth of about 0.3 mm to a flat floor of a remarkable character. This depression was, however, occupied during life by a mosaic of small plates of very nearly that thickness. These plates have the same histological structure, and are of the same thickness, as that part of the ordinary head shield which Stensiö has shown to have been laid down within the chorium.

There thus remains only a very small space, probably less than 0.1 mm, between the cover plates and the bony floor of the lateral field. The cover plates are loose, for they have invariably dropped out in isolated cephalaspid heads and are in fact only preserved in those very few cases in which a complete *Cephalaspis* with its body has been preserved, and even so in some cases the plating of the lateral field may fall away. The lateral plates are polygonal, fit with extreme accuracy as a mosaic, and leave no holes whatsoever between them, and their persistence, unfused, can, I think, only mean that a flexible cover was necessary for the function of whatever organ lay below these plates.

The next problem is the actual nature of the very elaborate series of canals which pass to the lateral areas. These canals differ in their character. The greater number of them, and

\* As a non-committal term I propose to speak of 'the lateral field', though every part of this discussion applies, I think, equally well to the dorsal 'electric field'.

those which are smaller in diameter, were quite clearly filled with blood vessels. Stensiö has shown that both arteries and veins pass outwards to supply the regions of the lateral field, and as this supply forms part of the very elaborate pattern of the blood vessels of the head as a whole there can be no doubt that he is correct.

Within the actual areas there is an immense development of such canals in a way which implies the existence of a great mass of blood which it is natural to assume was contained in capillaries. But in *Myxine* there are often no capillaries, small arterioles opening directly into great red-lymph spaces, and the conditions in *Cephalaspis* may well have been similar. The distinction in *Cephalaspis* between blood spaces and lymph spaces can certainly not be made on the skeleton alone, and the same thing may in fact be said about *Myxine*, where Cole has given an admirable account of the whole extraordinary structure, showing that there is a great lacuna system, including the so-called red lymphatics, which are in fact filled with red blood, and true white lymphatics which discharge into the enormous red subcutaneous sinus.

It is very difficult to understand why *Myxine* and, apparently, *Cephalaspis* find it necessary to have such an enormous blood volume. At any rate the appearance of the lateral fields in cephalaspids suggests that the flexible roof rested upon a great pad of lacuna tissue, filled perhaps with blood, perhaps with lymph, and hence providing a locally compressible support for the cover plates. In other words the cover plating, if pressed in locally, would merely drive blood or lymph to some other part of the area.

The other series of canals supplying the lateral areas are those, described by Stensiö, which he considered to have been occupied by nerves passing to the electric organ he expected to find in the field. Stensiö's text-figure 43 (Stensiö 1927, p. 201) shows how extremely unlike normal nerve canals these structures are. The canals containing what Stensiö assumes to be the effector nerves to the electric organs arise from the extreme lower part of the cavity for the vestibule of the inner ear. They separate from one another and their branching begins at, or very nearly at, the inner border of the lateral field, and it continues in such a way as to distribute branches over the length of the whole field, five separate lengths of the field in most cases being supplied by independent main trunks. The character of this branching and the termination of the branches is highly peculiar. Whilst the canals concerned with blood supply radiate from centres in the middle of the field over the whole width of the area, the individual terminal twigs being of very small diameter, the relatively immense canals from the ear never pass into really fine canals, but appear to end abruptly, and indeed to have an ending which, so far as can be judged in the broken material, is almost as if the end of the tube had been sliced off, leaving a groove on the bony floor extending beyond the end of the roof of the terminal canal. The actual endings of these canals lie in general (and perhaps exclusively) very close to the lateral border of the lateral area. They pass underneath the greater part of the structure without opening—at least such seems to be the general condition. I think that Stensiö is mistaken in representing anastomoses between the terminal parts of these canals in his text-figure 28 (1927). It is evident in many specimens that a continuous thin sheet of bone connects the branches, the canals being in effect excavated in its substance so that they cause local thickenings which separate grooves on the outer surface of the sheet. These grooves may very readily be mistaken for ducts, whose upper part has been broken away. Inspection of his figure 18 of the

model of the labyrinth cavity of *C. hoeli* (Stensiö 1927, text-figure 18, p. 79) not only makes the general character of the roots of these canals evident, but makes clear also the very remarkable fact that many of the individual canal roots are of larger diameter than the foramen through which pass the whole of the VIIth and VIIIth nerves on their way from the brain to the ear. Taken together the area of transverse section of the canals which conveyed 'electric nerves' must be at least five times that of the internal auditory meatus through which the VIIth and VIIIth nerves gained entrance to the ear capsule. This being so it is exceedingly difficult to believe that the so-called nerve canals can in fact have served a nerve, for their disproportionately large size is too obvious. Similarly the canal supposed to be for the electric nerves to the dorsal field is very considerably larger, twice as great in area as that for the nerves which serve the whole structure of the ear.

Stensiö recognized the difficulty presented by the extreme shallowness of the space which must have been occupied by his electric organ. Westoll emphasizes this, and makes the suggestion that it must have housed those parts of the lateral-line system which are absent in cephalaspids. Westoll's view seems to me impracticable because the cover plates fit with such extreme accuracy, leaving no pores between them, making it very difficult to see how pressure changes could be conveyed to neuromast organs.

I therefore make very tentatively a new suggestion as to their function, which has some similarity to that of Westoll. I have pointed out above that the actual structure of the lateral area implies that its roof was flexible, and the possibility of local depression of the roof is kept open by the presence of great blood- or lymph-filled spaces immediately below the cover plates. I have shown above that the size of the canals passing from ear to the lateral area is so great that they cannot possibly have conveyed nerves. The fact that the openings of these canals lie entirely along one side of the lateral area suggests that it was only there that any part of the apparatus which perhaps functioned as a sense organ could have lain. The suggestion may therefore be made that the canals housed tubular extensions of the labyrinth, perhaps filled with perilymph, perhaps with endolymph; that these at the proximal end lay within the ear capsule and were provided with neuromast organs; and that the terminal twigs of the tubes, so much larger than the canals filled with blood vessels in the neighbourhood, ended in little ampullae which could be pressed in by the passage of a pulse of pressure over the surface of the cover plates, the resulting flow of water along the tube directly affecting the neuromast organ which lay at its base, the pressure inside the internal ear being presumably equalized by flow of water along one of the neighbouring canals which ended in a region of decreased pressure. Such an apparatus would provide a machinery for the recognition and localization of the source of any pressure waves set up in the water in which the creature was swimming, and would thus in effect replace the lost parts of the lateral-line system.

A partial analogue can be found in the arrangement whereby the Weberian ossicles convey wave movements to the ear in cypridiformes.

#### RESTORATION OF POST-CRANIAL SOFT ANATOMY

Examination of the drawings of the restored head of *Cephalaspis* (figures 1, 2 and 3) must inevitably raise many problems of the structure of the various organs which were contained in it.



So far as the head itself is concerned Stensiö seems to me to have solved all problems of importance as to which there is evidence, but the structures lying behind and above the suprabranchial shield deserved further consideration. In *Kiaeraspis* the large hole through which in *Cephalaspis* the oesophagus and the ventral aorta passed is divided into two, thus confirming the identification. Thus the oesophagus passes backward, immediately dorsal to the ventral aorta, and it should be possible to determine the mutual positions of the heart and gut in the trunk.

Stensiö's figures and models show with certainty where the spinal cord, vertebral column and dorsal aorta lay at the back of the skull. It is evident (Stensiö 1927, text-figure 13) that after it has passed through the post-branchial wall the median dorsal aorta passes to the right side of the vertebral column and dorsally, so as to show the limit of the muscular body wall and the visceral cavity. This in turn fixes the position of the post-cardinal veins, which always lie as far dorsally as possible in the body cavity. These are usually continued forward as anterior cardinals, the Cuvierian duct being connected to their junction. In cephalaspids the anterior cardinal is not known, but the course of the vena capitis lateralis, one of its important factors, is and suggests that the vessel passed backwards dorsally and laterally entering the body cavity in direct continuity with the posterior cardinal, about at the level where the dorsal aorta leaves the middle line. The immense marginal vein is the chief factor of the jugular vein, and its entrance into the body cavity is known. Thus it is natural to suppose that there were a pair of Cuvierian ducts leading to a sinus venosus, which lay entirely dorsal to the level of the pharynx.

The pharynx, where it passes through the post-branchial wall in *Cephalaspis*, is wide in proportion to its depth, presumably because the opening for its passage includes the origin of the internal ducts to the last pair of gills. The opening is a little asymmetrical, which may mean that the oesophagus immediately on entering the body cavity turned to the left.

There remain for consideration the three backwardly directed thin bony sheets which project into the body cavity from the post-branchial wall, immediately above the oesophagus. These were interpreted by Stensiö as having housed the anterior end of the pronephros, which in cyclostomes is large, with openings into the pericardium. This explanation seems improbable, for the whole kidney system of, for example, *Myxine* lies in the closest connexion with the posterior cardinal vein, which is far removed from the structures under discussion.

The head of *Cephalaspis* is remarkable for the immense size of the spaces occupied by veins, and their very irregular shape. This presumably implies that, as in *Myxine* (and *Petromyzon*), there was little or no distinction between veins and lymphatics, and a very large blood volume. The irregular shape of these 'venous' spaces certainly implies a negligible venous blood pressure at the sinus venosus, and means that the heart must have been a suction pump, or that there was a development of 'subsidiary hearts', as in *Myxine*, to return the venous blood.

In *Petromyzon*, in contrast with *Myxine*, the pericardium has a rigid wall made by a cartilaginous cup at the posterior end of the branchial basket, and the portal hearts are absent.

· Is it possible that the three sheets of bone which certainly lie in the region of the heart gave attachment to sheets of membrane which, suitably attached to rigid structures elsewhere, provided the fixed volume pericardium which seems so desirable? If so it is obvious



from the asymmetry of the structures that the characteristic cyclostome one-sided heart was in process of being established, the whole being displaced to the right. Thus it is not unlikely that an asymmetrical heart in a pericardium on the right side, and an oesophagus on the left, with the anterior end of the liver, filled up the space within that anterior part of the trunk which in *Kiaeraspis*, for example, becomes surrounded by fused rows of scales, which render any trunk musculature within them useless.

A new study of ostracoderms, based necessarily on materials presented by Dr E. A. Stensiö and others, but making use of new materials, thus in nearly all important ways confirms Dr Stensiö's conclusions, but suggests some modifications of interest and novelty.

My thanks are due to University College, London, for the hospitality of the Department of Zoology, to Professor Medawar and his staff for constant help, and especially to Miss J. Townend, who drew the figures which illustrate this paper and suggested many improvements in its presentation. To the Royal Society I owe Miss Townend's help.

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