III.—A Monograph on the general Morphology of the Myxinoid Fishes, based on a study of Myxine. Part V. The Anatomy of the Gut and its Appendages.

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CONTENTS.

The first four parts of this work, on the skeleton, muscles, and vascular system, were published in the *Transactions* of the Society in 1905, 1907, 1909, and 1912.

The present section does not include the teeth, which, belonging properly to the skin, will be described when the skin and its appendages are dealt with. It will be noticed from time to time that I have to record striking differences from results obtained by other authors. Such differences must, of course, be recorded; but in recording them it must not be understood, unless the contrary is expressly stated, that the observations under discussion are necessarily inaccurate. One cannot investigate Myxinoid anatomy without frequently coming up against somewhat astonishing variations, and I have long been convinced that there must be races or colonies of *Myxine* which have not been distinguished specifically, but which, nevertheless, possess anatomical features in common. To give one instance out of many. Mr R. H. Burne has described in detail an anal slime gland in *Myxine*. In my sections of examples up to 25 cm. there is no trace of this structure. On examining Mr Burne's sections I find that the dorsal chamber of the cloaca has been converted into what anyone would interpret as a slime gland, similar to the series at the side of the body developed in connection with the skin. Mr Burne, therefore, is both right and wrong at the same time, but no one with the material at his disposal could have deduced what the supposed anal slime sac really was.

I must express my indebtedness to Professor A. Meek and his assistant, Mr B. Storrow, for their very successful efforts to obtain living specimens of *Myxine*, and for the hospitality of the excellent marine laboratory at Cullercoats. The experiments on the bio-chemistry of the liver were carried out by my museum assistant, Mr A. H. Malpas.

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A. Habits of Myxine.

The predaceous habits of *Myxine* have been known for a long time. Linnæus, who classified it among the "vermes intestina," says: "Habitat in Oceano europæo, pisces intrans, devorans, aquam in gluten vertens." Pennant, in 1766, refers to the fish on the lines being reduced to skin and bone by *Myxine*.

At Cullercoats *Myxine* is found on a muddy bottom, not as a rule inside the 23-fathom line, and common at 25 fathoms. It also occurs on a clayey bottom from 25 to 50 fathoms, but is not so numerous. On their own ground they must be as plentiful as earthworms. They will migrate on to an artificial muddy bottom, such as when a quantity of dredged mud has been dropped by hoppers on to an originally hard bottom, and in one such case they were known to have moved inshore from 6 to 3 miles.

All fishermen agree that the Hag enters the line fish by the gills and not by the mouth, and completely cleans it out, so that when the hooked fish is hauled up it is simply a bag of skin and bone. This was described by Fleming in 1823, and Meynell mentions that 123 *Myxine* were taken out of one codfish at Redcar in 1843. At one time *Myxine* were so common as to constitute a serious menace to the line fishery, but the fishermen allege that since trawling has developed, the Hags have largely disappeared, due doubtless, if correct, to the trawlers reducing the food of the Hags. It is further asserted by the fishermen that *Myxine* will not touch a fish that has been long dead, but that they only attack dying or newly dead line fish. They are readily captured on hooks baited with the foot of the limpet and salt herring.

The Hag swims freely and easily, like an eel, by lateral undulations. It can swim backwards, and usually escapes from a bucket tail first. Its power of secreting slime has been greatly exaggerated, unless the extensive experience which I have now had is greatly at fault. Goode and Bean state: "A single Hag will fill a two-gallon bucket with slime mingled with water in a few seconds, and after a slight interval can repeat the operation with ease." I have seen nothing in any sense approaching this performance.

Owing to the fact that hooked *Myxine* are usually damaged by the hook—in some cases the hook may be found as far back as the anus—I devised the following method of capturing large numbers of Hags in 1903. A line about a quarter of a mile long with, say, 35 black jack (*Gadus virens*) tied to it at intervals was anchored at each end to the sea bottom in 25 fathoms of water. From the anchor at each end a line with a float went to the surface, so that the position of the bottom line could be located. The bait must not be left down too long—in three hours, for example, all the black jack would be destroyed and the Hags gone. In this and other experiments I was able to establish:—

1. That *Myxine* never attacked *living* fish on the lines, but preferred fish recently living to stale fish. They did, indeed, attack the latter, thus disproving the assertion of the fishermen. I agree, however, with the fishermen that Hags never attack living free swimming fish, and are therefore not parasites.

2. As indicated by the slime, the Hags enter the fish by the gills rather than by the mouth. This, doubtless, to escape the teeth. When the fish were hauled up the Hags could be seen sticking out of them in all directions, and great numbers were lost by escape through the mouth. Only a few came out through the gills.

3. The body cavity was usually entered dorso-laterally. The liver was eaten first, then the gut and heart, and finally the flesh between the skin and backbone was attacked at the posterior end of the body cavity, the Hags working forwards until the dorsal muscles were entirely devoured. The whole operation takes about two hours.

4. In a dying or feeble fish the Hags stop the action of the gill cover by blocking it with slime. As soon as the motion of the operculum ceases, they enter the body through the gills.

5. It was invariably noticed that in the region of the back the Hags did not touch the spinal nerves, which looked as if they had been roughly dissected out. This, I believe, is not due to any preference for muscle, but simply owing to the peculiar character and action of the dental apparatus, which would rasp away the muscle and leave the stringy nerves.

The respiratory current in *Myxine* is easily demonstrated in the living animal by placing a few grains of eosin in front of the nasal aperture. Almost immediately water discoloured by eosin will be seen issuing from the branchial apertures. The respiratory current is a constant and steady stream, and there is only occasionally a sharp discharge from the gills.

Myxine can evidently distinguish light from darkness. When a number were placed in a large tank with one dark end, all the more active and healthy fish migrated to the dark end, and invariably returned there when brought back.

B. Nasal Aperture and Mouth.

The nasal aperture is relatively very large, as in *Palæospondylus*, and is median, dorsal and terminal. It is compressed from side to side, and is overhung above by a prominent forwardly projecting lip-like process. On each side of the latter is a short anteriorly projecting pointed tentacle for anterior touch, and below and in front of it, but at the side of the nasal aperture, is another and similar tentacle on each side. In the living animal the latter tentacle juts out almost at right angles to the long axis of the body and somewhat downwards, and is for lateral touch.

The mouth is circular and sub-terminal. There are no obvious jaws. It is situated on the ventral surface behind and below the nasal aperture. In both dead

and living specimens it is contracted and puckered at the edges. At the sides of the mouth, somewhat in front, is a long slender tentacle (the longest on the head), which is directed in a curve downwards and either forwards or backwards. This tentacle can be rotated forwards, and is for ventral touch. Internal and posterior to this on each side is a smaller tentacle with a very expanded base. From the dorsal front border of the mouth in preserved specimens two prominent diminishing ridges pass backwards into the mouth. There is no buccal funnel as in *Petromyzon*.

C. The Body Cavity.

When a median ventral incision is made, and the body walls reflected, we note, first of all, the peritoneum—a thin, glistening membrane lining the body cavity, and through which the muscles of the body wall are plainly visible. Anteriorly in the body cavity are seen the two lobes of the liver, one behind the other, the posterior lobe being rarely partially subdivided into two, whilst between these two lobes on the right a portion of the large gall-bladder projects. The very wide and perfectly straight intestine is noticed passing back to the cloaca from over the posterior lobe of the liver. To the right of the intestine is usually seen the single gonad (*i.e.* its ovarian portion), which in the individuals predominantly female more or less affects the shape of the intestine according to the time of year. This part of the gonad is formed in a genital duplication of the dorsal mesentery (mesoarium) on the right side only (cp. Part II., fig. 1), and thus corresponds to the right genital gland. In a female hermaphrodite the ovarian region of the gonad will be found to contain a number of very large elongated oval eggs, whilst in the male hermaphrodite it may not be seen at all without further examination.

If the posterior section of the intestine be examined carefully (fig. 5), it will be noticed that as it approaches the cloaca it begins to fuse at the mid-ventral line with the body wall—thus forming at the beginning of the fusion a rudimentary mid-ventral mesentery (*mes.'*). The fusion of the intestine with the body wall, however, at once extends obliquely upwards and backwards (*mes.''*), thus completely obliterating the body cavity below the intestine. The body cavity, hence confined to the roof of the gut, becomes diminished as it is continued backwards, and opens finally into the cloaca by the large, single, median porus genitalis or abdominal pore (*p.g.*), as elsewhere described.

The intestine is suspended by a median dorsal mesentery (*mes.*, cp. also Part II., fig. 1). As shown in fig. 5, this mesentery terminates by a curved border a short distance in front of the abdominal pore, and thus the two dorsal halves of the body cavity are in free communication for a short region anterior to the genital pore. This is obviously necessary in order that the large eggs may escape with facility.

If the anterior extremity of the body cavity be now examined on the right side, and the liver turned over to the left, it will be seen that the pericardial cœlom with its contained heart is situated over the anterior extremity of the front lobe of the liver,

and also that the latter cavity communicates with the body cavity on this, the right, side by a large pericardio-peritoneal foramen. This is the only one present, the pericardium being imperforate on the left side. There are, however, two foramina in the *Ammocœte*, but none in the adult *Petromyzon*. In a 34-cm. Hag the pericardio-peritoneal foramen was an elongated aperture 9 mm. long when slightly stretched, and was directed obliquely forwards from right to left. Its right wall is formed by the serosa of the gut, and here the very large supra-intestinal or portal vein (fig. 4, *p.v.*, and cp. also Part II., fig. 1), and in some cases even the portal heart (*p.h.*), projects boldly into the foramen. It is usually stated that the portal vein passes through the foramen on its way to the portal heart, but the vein lies morphologically outside the foramen, and is in fact only accidentally related to it. On the other hand, the common portal vein (*c.p.v.*) is neither apparently nor really associated with the foramen. The left wall of the latter is formed by a special duplicature of the peritoneum having a well-defined and slightly thickened free border. This structure, doubtless, corresponds to the Selachian pericardio-peritoneal septum. The presence of such a large pericardio-peritoneal foramen in *Myxine* is possibly correlated with the existence of an important pericardial pronephros.

A little behind the heart the intestine, which has so far been suspended by the median dorsal mesentery, takes an upward turn, and therefore the two sheets of the peritoneum, instead of becoming opposed to form the median mesentery, pass at once separately on to the gut, and from the gut they immediately reach the anterior lobe of the liver, instead of forming a median ventral hepatic ligament such as suspends the *posterior* lobe of the liver to the intestine. It is from these lateral sheets of peritoneum that the pericardium is derived. There is thus no discontinuity in the mesentery at the anterior end of the body cavity as there is at the rectum, apart, of course, from the pericardio-peritoneal foramen itself.

When the intestine is displaced to one side, four large vessels are seen attached to the body wall at the mid-dorsal line. The outermost pair are the segmental or pronephric ducts; the innermost, the two posterior cardinal veins. It will be noticed that of the two cardinals the right is perceptibly smaller than the left, as in *Bdellostoma*, and also in preserved specimens the left is the more usually blocked with blood. The dorsal aorta is hidden from view (except anteriorly) between, and dorsal to, the two cardinals, and is, as a rule, only exposed by dissection (but this varies). The arteries from the aorta to the alimentary canal and gonad (cp. Part II., fig. 1) are seen emerging between the two cardinals and apparently from them.

Almost at the mid-dorsal line of the whole length of the gut, and to the right of the attachment of the dorsal mesentery, courses the very large portal vein (Part II., fig. 1, *p.v.*).

The anterior region of the body cavity, with the opening from the abdominal into the pericardial cœlom is figured by GOODRICH (24, p. 44) in *Myxine glutinosa*.

D. The Respiratory Organs (Figs. 2, 6, and 12).

The coarse anatomy of the breathing apparatus of the Myxinoids has been so often described that an acquaintance with it may be taken for granted. Further, the general structure is sufficiently indicated in the reconstruction given as fig. 2. The peribranchial or pleural sacs, and the relations of the gills to them, are fully described in my Part IV. pp. 220–222. I may, therefore, at once proceed to a more detailed account of the anatomy of the parts.

1. *Structure of the Gills.*

Under the serous membrane with its long flat nuclei the outer gill wall exhibits a loose connective-tissue layer in which muscle fibres are lodged. They are in two sparse layers, an external circular or concentric, the axes being the gill ducts, and an internal radial. The concentric fibres do not pass right round the gill, but each bundle of fibres forms only a more or less short segment of the circle. The fibres histologically are intermediate between the plasmic and aplasmic types described in my second part. They are distinctly striated; the nuclei are large, vesicular, and peripheral; but there is only a slight quantity of sarcosplasm present, most of it being collected round the nucleus. The fibres are somewhat flattened, and average about 37·5 μ by 12 μ, and both the transverse and longitudinal striation show up with diagrammatic clearness in material stained with iron hæmatoxylin.

The fundamental *ground plan of the Myxinoid gill* is quite simple. There is a tube connecting the gut with the exterior, which we may call the *gill duct.* At one place the epithelial lining of this duct throws out a number of lamelliform evaginations —about 8–10, but the number in the adult is difficult to enumerate owing to secondary modifications—the long axes of which are radial and the short axes parallel to the long axis of the duct. Hence at this place a considerable swelling of the duct supervenes to form the cake- or pouch-like gill. The unmodified proximal and distal portions of the duct remain as the *afferent* and *efferent gill ducts* respectively (figs. 2, 6, and 12, *a.g.d.*, *e.g.d.*)

It therefore results in a section at right angles to the long axis of the duct itself that we have a star-shaped arrangement. There is a central cavity, the cavity of the duct, and a number of compressed radial chambers opening into it. The tissue between the walls of contiguous evaginations is highly vascular, and constitutes the respiratory apparatus of the gill. This tissue projects inwards from the outer wall or periphery of the gill as a number of radial plates, each one clothed by two sheets of epithelium—the walls of two adjacent evaginations. A *gill lamella*, therefore, is formed by the contiguous walls of two epithelial evaginations plus the intervening vascular tissue.

The afferent gill artery (*af.br.*), on reaching the gill, forms a circle round the efferent gill-duct (cp. fig. 6). From this circle a number of radial arteries arise like the

spokes of a wheel. These are easily seen in an injected gill coursing quite close to the outer or more convex surface of the gill from the centre to the edge. The radial arteries in their turn give off a number of vessels at right angles which travel in the core of the gill lamella between the epithelial sheets above mentioned, and join up to form, on the inner or less convex (sometimes concave) surface of the gill, another series of radial or spoke-like arteries, which all open into a further circular vessel round the afferent gill duct. From the latter circle the two efferent branchial arteries (*ef.br.*) arise, and behave as described and figured in my Part IV.

The actual structure of the gill, however, is not as simple as this. The radial epithelial evaginations, for example, often dichotomise at least twice, and sometimes five times—twice in the lateral regions of the gill (*i.e.* near the afferent and efferent surfaces), and five times in the central region. This produces at the circular margin of the gill a large number of diverticula instead of a few. Then the radial vessels connected with the rings round the afferent and efferent gill ducts anastomose and branch. Again, the respiratory surface of the gill lamellæ does not remain simple and smooth. A number of ridges or pleats are thrown out which themselves dichotomise several times along their long axes so as to produce in transverse section a dendritic appearance—not, however, over the whole of the gill lamella, for, axially and especially laterally, *i.e.* nearer the greater gill surfaces, the gill lamella remains smooth. The same result would, of course, be produced by a series of *ingrowths* of the epithelial covering of the lamella, and this is perhaps how the dendritic structure seen in transverse section has arisen.

The ridges or pleats stretch straight across the gill lamella from one surface of the gill to the other, at right angles to the greater surfaces of the gill. Hence, they are cut longitudinally in transverse and horizontal sections of the gill, and transversely in vertical sections. Hence also the dendritic structure is only obvious in vertical sections.

A vertical section of a well-injected Myxinoid gill is a beautiful but deceptive object. One sees what appears to be a number of radial vessels converging inwards from the periphery to the centre of the gill. Proximally these vessels are simple in structure, but as they approach the centre of the gill they become highly dendritic. Lateral branches are given off which bifurcate a number of times. There is apparently no question of arteries and veins. Each branch lodges only one vessel, and therefore seems to be a vascular *cul-de-sac*.

A closer examination and comparison with sections in other planes reveals the explanation. Proximally each lamella exhibits in vertical section *a linear series of vessels cut in transverse section*. These are often connected up by vertical anastomoses, and this conveys, in vertical section, the wholly false impression of a radial vessel. The dendritic structure is again equally misleading. Here also, so far from having vascular *culs-de-sac*, we have in reality a large number of transverse sections of very small vessels *coursing at right angles to the plane of the section* from one large surface of the gill to the other, and connected up at right angles by innumerable branching anastomoses. In a *transverse* section these anastomoses show very well as extensive aggregations of

massed dots in the more central portions of the gill. We have, in fact, a definite capillary system in the gills, although a somewhat coarse one. Near the circular margin of the gill a few respiratory vessels may pass straight across from the afferent to the efferent radial vessel without modification, as shown in fig. 6. The type of gill circulation described above, carried much further, gives us the example of circulation found in the gills of the lamprey as described by FAVARO.*

The branches of the afferent radial vessel do not usually pass straight across the gill to become the factors of the efferent radial. Sometimes they do, and one can then trace across the gill lamella a single vessel coursing from the afferent to the efferent vascular side of the gill, and giving off anastomoses (about 50) as it goes along. But more frequently the direct continuity is broken, and the branches of the afferent radial interdigitate with the factors of the efferent vessel, as shown in fig. 6.

In section it is easy to distinguish within the gill the branches of the afferent branchial artery from the factors of the efferent branchial. The walls of both include a few unstriated muscle fibres with long flat nuclei, but the lining of the afferent vessels is very characteristic. Here we find, projecting into the cavity of the radial vessels and their branches, large cells of varying shape separated from each other by distinct intervals. They may project 12 μ into the cavity of the artery, and are separated by spaces of about 2·5 μ, but sometimes by much wider gaps. At their base they are about 10 μ across. Each cell contains a large vesicular nucleus—sometimes two —and the cytoplasm lodges a number of yellow brown particles not coloured by all dyes, but staining black with iron hæmatoxylin.

These cells evidently constitute a blood "gland" of some kind. GIGLIO-TOS regards the lymphoid tissue of the valvula spiralis of the Ammocœte as the source of both red and white corpuscles of the blood; but this view is attacked by ASCOLI, who regards the circulating blood of the Ammocœte as the formative sphere of the red corpuscles, as in the embyro, and finds, as K. E. SHREINER has also done in *Myxine*, the new corpuscles dividing in the blood. MAAS admits his inability to trace the source of the red corpuscles of *Myxine*, and was not able to observe any early stages in the blood. He states, however, that the body of these corpuscles, stained with iron hæmatoxylin, exhibits numerous dark small accretions. I hope to be able to show in my next part that the lining cells of the afferent vessels of the gills described above are the source of the red corpuscles of the blood.

Besides the afferent and efferent arteries the connective tissue of the gill lodges a large number of irregular spaces, or *lymphatics*, having an inconspicuous but definite lining with flat nuclei. Usually these spaces contain only a few blood corpuscles, but they may contain many. They partially fill up in injected material. They are found not only in the wall of the gill, but extend also into the coarser portions of the gill lamellæ. On the side of the efferent gill duct the lymphatics communicate with the peribranchial sinus (cp. Part IV. p. 221) by a large but short channel, which enters the

* *Atti Accad. Sci. venet. trent. istr.*, 1905.

gill in company with the afferent branchial artery. Similarly, both the efferent branchial arteries of a gill are associated with lymph channels placing the lymphatic spaces on that side of the gill in communication with the dorsal sinus system (cp. Part IV. pp. 220–1), but the lymphatics are not so well developed on this side of the gill.

The large *mucous cells*, which are so characteristic of the Myxinoid gill gut do not occur within the gills themselves. In one case, however, I found numerous mucous cells of the glassy type in the thicker epithelium on the efferent gill-duct side of the gill.

The whole of the complex cavity of the gill is lined by *epithelium*, which is better developed near the two great surfaces of the gill, where the gill lamellæ are simple in structure, and which, further, is stronger on the afferent arterial side than the efferent. There is roughly an extra rank of nuclei on the afferent side, and in some specimens the disproportion is greater than this. The free surface in places is bounded by flattened squamous cells, and under these there may be up to four irregular ranks of nuclei, some of which here and there are observed to be undergoing mitosis. The cell boundaries can be easily distinguished under the higher powers of the microscope, the epithelium then having in vertical section the appearance of a mosaic.

In the complex or more respiratory portions of the gill lamella the blood is only separated from the water by what appears to be, in longitudinal sections of the vessel, a single row of shallow cells about 2 μ thick, and having flattened nuclei up to 10 μ long, separated by intervals of 20 μ. In transverse sections of the vessels these nuclei are seen to follow the curves of the vessel, and are hence markedly crescentic. They measure about 10 μ this way also, and are therefore circular concavo-convex discs. Under the highest powers of the microscope, however, this boundary separating water from blood appears as a very thin, almost structureless, membrane having definite outer and inner borders, the nuclei above described being situated on the vascular side, and internal to the inner border. The above statements apply only to that part of the vessel which projects or bulges into the cavity of the gill, *i.e.* that portion of it in direct contact with water. Elsewhere the nuclei are of a different character, and are embedded in the wall of the vessel.

Although appearances very often suggest it, I have not satisfied myself of the existence of intra-cellular capillaries in the Myxinoid gill.

The *efferent gill duct* is lined internally by a layer of mucosa thrown into about twelve conspicuous folds. Underneath this is a somewhat extensive vascular zone of fibrous connective tissue forming the submucosa. This in its turn is surrounded by the irregular but well-developed muscular coat of striated fibres, of which the external fibres are mostly circular and the internal ones longitudinal. External to the muscular coat we have no definite boundary, but some very loose fatty connective tissue. The lining epithelium is very similar to that of the gill itself: there are about three ranks of nuclei; cell boundaries are easily distinguishable in methyl-blue-eosin preparations—the superficial row of cells being flattened, the cytoplasm vacuolated, with a definite

free border. Occasional mitoses are seen, but there are no gland or mucous cells. A few of the glassy mucous cells were, however, seen in the *afferent* gill duct, and SCHREINER says that there are "by far not as many slime cells in the afferent gill ducts as in the mouth." The muscle fibres are, on the whole, similar to those of the gills, except that they are coarser, and the striation is not so distinct.

The *external branchial apertures* are conspicuous openings situated far back near the middle line on the ventral surface, just in front of the anterior extremity of the pre-anal "fin," and a little behind the anterior third of the body. They are always asymmetrical as regards size, but not invariably so as regards position. The right is always the smaller of the two (and naturally so, as the ductus œsophago-cutaneus only occurs on the left side), and it is situated a little in front of the left; externally the left opening is sometimes partially, but rarely completely, divided into two—in the latter case the ductus œsophago-cutaneus having a separate external aperture. In 1815 Sir EVERARD HOME published a figure by WILLIAM CLIFT in which three such openings are indicated. J. MÜLLER, however, states that he has never seen this, but MAAS finds in his youngest specimens the branchial cloaca and the ductus œsophago-cutaneus entirely separate, so that only their openings on to the outer skin come together, like a pair of spectacles. He supposes therefore that the common duct is only formed with age, but adds that the ductus never opens medially, but always on the left. There is no doubt in fact that the ductus is a potential *left* gill. When the ductus opens separately the two apertures are not side by side, as in CLIFT'S figure, but antero-posterior, the smaller anterior one being the orifice of the branchial cloaca of its side, and the larger posterior one that of the ductus. Internally, of course, the two structures are always distinct.

The structure of the gill of *Bdellostoma* has been described by JACKSON (30). He has evidently, however, directed but little attention to this section of his work, and his scheme of the circulation, representing, as it does, one side of the gill as arterial and the other as venous, is manifestly unsound even on *a priori* grounds. He has failed here to recognise the fundamental fact of the interdigitation of the afferent and efferent vessels —a condition absolutely essential if the gill is to be a respiratory organ at all. Again, his fig. VIII. is a misinterpretation of the apparent dendritic structure of the gill lamella as seen in vertical section. As I have pointed out above, it is fatally easy to commit this error, especially if one does not realise how impossible vascular *culs-de-sac* must be in the Chordate gill.

The development of the Myxinoid gill follows the course we should deduce from a knowledge of its anatomy. In *Bdellostoma*, according to STOCKARD (52), the gill is originally tubular, only the œsophago-cutaneus duct remaining in the tubular stage throughout life. The gill tubes are entirely endodermal. At the point where the future gill pouch is to develop the lumen of the tube becomes enlarged, and then, by a folding of the walls, the characteristic radiate gill is produced as outlined in the anatomical description above.

2. *Variations in the Number and Vascular Supply of the Gills.*

Amongst the many dissections of the gills which I have made, the following departures from the normal number of six on each side were encountered :—

(*a*) *Seven gills on the left side.*—The additional one was apparently the last, since it was supplied by a twig from the last afferent branchial artery. Normal on the right side. In this specimen the ventral aorta was continued forwards as an impaired artery on to the club muscle.

(*b*) *Seven gills on both sides.*—On the left side all the gills were of much the same size, except that the middle ones were slightly the larger, and there were five afferent branchial arteries. The first and last afferent branchials split quite near their origin, to supply two gills each. On the right side the gills alternated with those of the left, the first being situated between the first and second of the left side, and so on backwards. The size of the gills was the same as on the other side, except that the last was very small, and only about one-third the dimensions of the sixth. There were six afferent branchials on this side, one to each gill, but the last small gill was supplied by a twig from the sixth, given off near the place where it entered the sixth gill.

(*c*) *Seven gills on the left side.*—First gill more anterior and rather more dorsal than usual, and situated laterally and dorsally to the posterior end of the club muscle, not reaching as far back as the latter point. Usually about half the first gill overlaps the club muscle, but the forward position above described may occur without any variation in the gills. Last or seventh gill much the smallest, and apparently the extra gill, as it is supplied by a branch of the last or sixth afferent branchial. Ductus œsophago-cutaneus present. Gills normal on the right side.

(*d*) *Seven gills on the left side.*—Similar case in every respect to (*c*), except that the afferent branchial for the seventh gill arose from the aorta side by side with the sixth, and was not merely a branch of the latter. The extra gill is again the smallest, but the disparity is not so great as in preceding case. Gills normal on the right side.

(*e*) *Seven gills on both sides.*—On the left the first is in a much more dorsal position than the others, and lies at the side of the club-shaped muscle, which latter projected slightly behind the posterior border of the gill. First afferent branchial split to supply the first two gills. Apart from the usual decrease in size from before backwards, the seventh gill was quite normal, and had its own afferent branchial—well separated from the artery supplying the sixth gill. On the right side the first gill does not differ in position from the others, but the whole seven form a graduated series of which the last is the smallest, but not remarkably small. Each of the seven gills was supplied by an afferent branchial artery arising separately from the aorta.

(*f*) *Seven gills on the left side.*—First rather more dorsal than the others, and lies at the side of the club muscle, which projects slightly behind it. First afferent branchial splits into two to supply the first two gills. Last gill distinctly smaller than

the others, and more ventral. It has its own afferent artery quite distinct from the one in front. Gills normal on the right side.

(*g*) Gills normal on both sides, but only five afferent branchials arose from the aorta. The last, however, on each side split almost immediately to supply the last two gills.

(*h*) *Seven gills on the left side.*—Other conditions exactly as in (*c*).

(*i*) *Seven gills on the left side.*—Other conditions as in (*c*).

It thus appears that the usual variation is the presence of an extra gill on the left side, the ductus œsophago-cutaneus being still present and opening independently. The case described by HOWES is one such, but the one mentioned by BATESON had seven pairs of gills and a ductus. HOWES considers that the extra left pouch is the ductus œsophago-cutaneus converted into a gill, so that the new feature in the varying animal is the ductus. This, of course, is quite possible, although it does not explain the additional gill on the right side, where no ductus has ever been found. We have therefore in *Myxine* the potential existence of a pair of gills behind the sixth + the ductus, which may conceivably represent an eighth pair.

E. THE MUCOUS SURFACES.

These are described from behind forwards, and as if the gut were split up along the longitudinal plane.

The *abdominal intestine* is a typical mid-gut, and is a straight and perfectly uniform tube in which regions cannot be distinguished either macro- or microscopically. It has a maximum width of 11 mm. in a 24-cm. Hag, and is moored to the roof of the abdominal cavity by a median dorsal mesentery (cp. Part II., fig. 1). Over the gut dorsally, and slightly to the right, are the gonad and the portal vein, and also the so-called sympathetic nerve. The latter is the most median of the three; then comes the vein, and finally the gonad, which lies at first over and then laterally to the vein, as shown in the above figure. The walls of the vein are very thin, and the vessel is seen rather by its contents than by its walls. At more or less regular intervals the arterial supply is seen to pass on to the gut *via* the mesentery.

The mesentery is easily detachable from the mid-gut in preserved animals, and the gut itself, where its form is not distorted by the development of the ovarian portion of the gonad, and in front by the liver, is smooth, and almost spherical in transverse section. Its outer wall exhibits an elaborate pattern due to the ramification of the very extensive vascular supply of its curious lymphoid coat. This pattern characterises practically the whole length of the abdominal gut, but it is somewhat simplified for about 6 mm. in front of the anus—in other words, the lymphoid tissue is wanting in the region of the hind-gut, and it simplifies again gradually in the neighbourhood of the posterior lobe of the liver, and may be lost altogether about 10 mm. behind the opening of the bile duct.

If an incision be now made along the line of the portal vein, and the gut pinned out so as to expose the mucosa, it will be seen that the latter is only very slightly attached to the submucous coat in preserved material (cp. Part II., fig. 1), with the result that it very readily comes away. It is thrown into about ten prominent longitudinal zigzag folds. Most of these folds are continued directly into those of the *cloaca*, but dorsally, above the anus, the cloacal folds are independent structures, and also ventrally there are smaller secondary folds developed between the larger intestinal continuations. Very few of the folds of the mid-gut, in some specimens none at all, pass straight from one extremity of the gut to the other. They may bifurcate and join up again, so as to form an elongated loop, or they may bifurcate without rejoining, which latter happens more commonly anteriorly than posteriorly. Branches may be given off which themselves bifurcate, and this often occurs in the region of the liver, so as to produce there a more complex pattern.

Opposite the posterior extremity of the posterior lobe of the liver the gut begins to change its calibre,* and the folds to flatten and die away, so that for a short distance behind the opening of the bile duct the mucosa is thinner, and almost, but never quite, smooth. However opposite, or even slightly behind, the biliary aperture the folds rapidly increase in size and projection, and a short distance in front of the opening they again project considerably into the lumen of the gut. The aperture of the bile duct is situated directly in the course, and breaks the continuity, of one of the *ventral* folds.

The zigzagging of the folds of the intestine is often emphasised by very short transverse folds, which project from the apex of one bend, and fit into, but never join, the depression of a bend in the contiguous fold. The zigzags of neighbouring folds therefore alternate. The pattern of the mucosa is, however, best seen by removing it entire, which is only too easily done in the preserved gut, and examining its submucous surface. We then notice that the same pattern is exhibited, only, of course, in the form of a cast, in the submucosa itself, and here the short transverse folds are indicated in a very striking manner.

According to Maas (39), the section of the gut anterior to the abdominal intestine may be separated into two regions—an anterior region, or *true œsophagus*, extending from the ductus œsophago-cutaneus to the point of entrance of the gut into the body cavity, and a posterior indifferent region, or "*stomach*," the hinder boundary of which is the opening of the bile duct. The former region has about six folds, and its lining epithelium is stated by Maas to be of a character transitional between the many-layered "ecto-" and the single-layered "endo-dermis," whilst the lining of the "stomach" is truly endodermal, although its sub-mucosa is not that of typical mid-gut.†

The gut, which has narrowed down considerably by the time the opening of the bile duct is reached, is narrowest of all just in front of this opening, and it is here closely invested by the cardiac portion of the M. constrictor branchiarum et cardiæ.

* In most specimens it *widens* considerably here (cp. p. 311).

† But cp. p. 312.

There can be no doubt that the folds of this portion of the gut are directly continuous with those of the abdominal intestine (and doubtless, therefore, have developed from the same embryonic layer), which have never entirely disappeared in the flat region behind the bile duct. This section, however, is only continued as far anteriorly as the opening of the ductus œsophago-cutaneus, from which point forwards the character of the mucosa quite changes, and, judging from anatomical evidence only, might have developed from a different embryonic layer. Two at least of the folds are continued forwards directly on to the posterior lining of the ductus œsophago-cutaneus, where they are prolonged outwards to its external opening. The other folds of the ductus are some of them intrinsic, and some are continuous with folds belonging to the next anterior region of the gut. The ductus does not open directly into the gut, but rather into a small pocket-like evagination of the latter, which itself then opens into the gut at right angles to the ductus.

In front of the ductus œsophago-cutaneus is the *branchial gut* of MAAS. Its posterior boundary is the ductus, and its lining epithelium is quite "epidermal" in character, which is somewhat surprising, seeing that it cannot be stomodæal in origin, even if it represents morphologically a greatly elongated pharynx. Its mucosa exhibits more numerous, closely-set, and shallower folds, some of which are continuous, or fuse, with those of the afferent gill ducts. A disturbing factor here appears to be the apertures of the latter ducts, and the mucosa of the branchial gut becomes increasingly irregular from before backwards. This, however, cannot be entirely due to the exit of the gill ducts, since between the first two the mucosa presents almost the same appearance as it does in front. But behind this point the pattern is complicated by the folds here and there gradually approximating, joining, or being connected up by numerous short, shallow, transverse ridges. The result is that there is a suggestion of a honeycomb mucosa at this region of the gut. Here also the wall of the gut is very thin, and the mucosa not detachable as in the abdominal intestine.

In front of the gill region, which must, from its development, be regarded as *secondary branchial gut*, the mucosa presents a very regular appearance, and there are about fifteen moderately prominent and perfectly straight longitudinal folds. These folds, however, do not always pass continuously from one end of this section of the gut to the other, but here and there die down, and are replaced by others. Opposite the posterior free extremity of the pharyngeal velum the folds tend to anastomose so as to form a simple honeycomb pattern, and they here terminate—none of them being prolonged into the mouth.

The *velum*, or *pharyngeal valve*, according to HUXLEY, marks off the posterior boundary of the mouth. It may be described as an extensive flat dorsal duplication of the mucosa, situated just behind the dental apparatus, when the latter has been withdrawn, and attached to the mucosa of the roof of the mouth by its mid-dorsal surface in much the same way as the gut is suspended by the mesentery. Now, this suspensory fold is prolonged backwards *behind* the region of the velum, and passes insensibly without

any break into the median dorsal fold of the œsophageal mucosa. The velum may thus be, and actually is, in one sense, merely the differentiated anterior extremity of the median dorsal fold of the œsophagus which has developed an elaborate skeletal support. On the other hand, the velum may represent the original roof of the gut cut off by lateral evaginations (cp. fig. 11). This agrees rather with the anatomical facts, and with what we know of the development of this structure.

The lateral edges of the velum are curled over sharply dorsally, and its posterior edge, when spread out, exhibits a short, blunt, median projection stiffened by the posterior transverse velar bar with its irregular posterior processes, and also on each side a pointed projection, the inner edge of which is supported by the termination of the internal lateral velar bar, and the outer or turned-over edge is strengthened by the external lateral velar bar. The ventral or flattened portion of the velum is sustained by the internal lateral velar bars and their anastomoses, whilst the dorsal doubled-over portions are stiffened at their edges by the external lateral velar bars. The median suspensory portion of the velum, which is more definitely developed behind than in front, is supported by the supra-pharyngeal skeleton associated with the anterior transverse velar bar (cp. Parts I., II., and III.).

The mucosa covering the velum is smooth.

If the *roof of the mouth* be examined, we find the mucosa thrown into coarse folds —probably due at least partly to contraction, since with preservatives such as Perenyi's fluid they are less obvious. Laterally in front are the conical third and the obtuse fourth tentacles. Just behind the latter in the mid-dorsal line will be found a pit, and rising from the bottom of this pit is an elevation of the mucosa, from the apex of which emerges the strongly curved, slender, median dorsal tooth. Immediately behind the level of the posterior margin of the dental apparatus (in the retracted condition) is a large deep recess, the ventral wall of which is formed by the mucosa of the roof of the mouth, which *apparently* terminates here in a somewhat irregular border, as figured by W. K. Parker (Pl. XIII., fig. 7), and the dorsal wall of which is formed by the base of the velum. This is the recess into which the naso-pharyngeal canal opens, and the latter aperture is seen if the free border above is drawn forwards. It is an elongated oval opening, wider in front than behind, and with an indefinite posterior border, owing to its being prolonged on to the base of the velum as a furrow, on which it is continued almost as far backwards as the anterior transverse velar bar. The mucosa, in fact, is doubled to form the border mentioned above, then becomes continuous with the mucous lining of the naso-pharyngeal canal at the posterior opening of the latter, is next continued on to the velum, and finally passes into the mucosa of the roof of the mouth and œsophagus behind the velum. On each side of the base of the velum dorsally and laterally is a deep, forwardly projecting pit with an almost smooth lining. Into the blind end of this pit a fold of mucosa projects in front. Sections, however, show *this* to be due to the root of the external lateral velar bar. The pit probably disappears when the dental apparatus is everted, and perhaps, therefore, only exists

when the latter is withdrawn. It is mentioned by J. MÜLLER. I do not find any special histological feature associated with it.

The lining of the *naso-pharyngeal canal* behind the nose is quite smooth and without valves. When the canal is split up and the nose examined from below, it is found that the median olfactory lamina is deeper and thicker, and has a more pronounced free margin than the others, and thus, in a sense, separates the apparently single nasal organ into two. The posterior portion of the third lamina from the middle on each side appears to have a somewhat valvular character, and would tend to direct water upwards among the laminæ in general. The lining of the *nasal tube* in front of the nose is almost smooth, and has no definite folds; but there is a well-defined transverse fold and a slight median dorsal longitudinal fold just in front of the nose itself, whilst dorsally and medially, just inside the external nasal opening, there is a blunt projection supported by a small independent cartilage (fig. 1, present part; and figs. 1, Parts I. and III.).

From the *floor of the mouth* there projects into its cavity the dental apparatus, consisting of two halves separated by a furrow or gutter. The mucosa is reflected over the bases of both rows of teeth, but more particularly over that of the outer row, whilst the two rows of each side are separated by another and very distinct fold of mucosa, the tips of the outer teeth being almost on a level with, or projecting slightly beyond, it. The dental apparatus is obviously a derivative of the mucosa of the floor of the mouth, and cannot move independently of it. Therefore, to admit of any movement at all, the mucosa in front of and behind it must be loose and ample. When the apparatus is withdrawn there is an obvious transverse folding or puckering of the posterior mucosa (which was previously on the stretch), whilst the mucosa in front is quite taut. Behind this give-and-take region the mucosa of the floor of the mouth is thin and almost smooth. Again, the margin of the mouth is always puckered when the dental apparatus has been withdrawn, but when it is everted there is a pleated area ventrally *outside* the mouth, which is not fully shown in any figure I have seen. In the retracted condition there is a raised zone of mucosa extending straight forwards over and in front of the protractor tendon, and which in places is very sharply folded—in fact, so much so that one often has to separate the lips of the depressions with a needle before they are noticed. These occur nowhere else in the mouth. They seem to me to be due to the fact that when the pre-dental mucosa is drawn into the mouth it is compelled to occupy a much narrower space laterally than it does when outside the mouth.

The mucosa of the floor of the mouth is practically smooth.

F. HISTOLOGY OF THE GUT.

The histology of the alimentary tract of *Myxine* has already been described and figured by K. E. SCHREINER, and especially by MAAS. The latter has investigated the

structure by the new methods of solution and digestion, using caustic alkali and pancreatic extract. I shall therefore confine myself to a general statement of the anatomy of the gut, supplemented by such new details as are necessary to amplify and elucidate the work already accomplished.

The gut of *Myxine* passes straight from mouth to anus. There are no obvious divisions into stomach, duodenum, and intestine. It is characterised by one very striking and unique feature. The mucous epithelium from the mouth to the entry of the gut into the abdominal cavity—that is, rather more than a third of its entire length —exhibits the peculiar and characteristic structure of the epidermis. The obvious explanation of this is that the whole of the lining of the anterior part of the gut is stomodæal in origin, but this we know to be not the case. The only other possible explanation, therefore—which is in fact no explanation at all—is that we have here a remarkable example of what is known as convergence. There can be no doubt that this anterior third of the gut represents an enormously elongated pharynx. It is pharyngeal in position in the embryo, but the interpolation of the club muscle during development detaches the gill-bearing region of the gut from the mouth, and results in the curiously posterior position of the gills in the adult.

There are two types of gut structure in *Myxine*. These we may call the pharyngeal gut and the abdominal gut. The former stretches from the mouth to the entrance of the gut into the abdominal cavity, and the latter continues the gut to the cloaca.

As an example of the *pharyngeal gut* or "œsophagus" we may take what MAAS calls the branchial gut. The mucous epithelium, which is many-layered, has just the character of the outer skin, and possesses in abundance both the clear glassy and the granular slime cells characteristic of the epidermis. MAAS distinguishes a stratum corneum and a stratum Malpighi, but, unless these terms are to acquire a new meaning, I do not see how they can be applied in this case. He also describes a muscularis mucosæ which goes far into the folds; but I find no trace whatever of this, nor, apparently, does SCHREINER. The submucosa is dense and fibrous, and with many lacunar blood spaces. According to MAAS, however, it consists of loose, very uniform, reticular cells with no lacunæ. Externally there is an obvious circular musculature of unstriated fibres. These fibres course *among* the dense connective tissue of the submucosa in its peripheral region. There are only a few isolated fibres, but they are easily seen, and they course right round the gut, taking no account of the folds of the mucosa.

According to SCHREINER, the mucosa has a basal membrane and exhibits no transverse folds in the "œsophagus," but these are certainly present in the branchial region. The superficial cells of the mucous epithelium give the slime reaction, and have a thin homogeneous cuticle. He finds a coiled thread in the granular slime cells, exactly as in the corresponding cells in the epidermis. I am unable to confirm this, in which I agree with HAACK. There are numerous mitoses in the mucosa.

In the *abdominal gut*, it is stated by MAAS that the folds of the mucosa have less projection, although this is not so in my preparations. He finds the ventral folds are

the better developed, but I agree with SCHREINER that the dorsal folds are usually the stronger. MAAS holds that the folds of the abdominal gut are not to be homologised either anatomically or physiologically with those of the pharyngeal gut, basing the distinction on the behaviour of the muscularis mucosæ, which I do not find anywhere in the gut, and on the assumption that the stratum compactum is confined to the abdominal gut, with which I do not agree. His assertion, therefore, that in the one case the folds of the mucosa do not affect the underlying tissues, but do in the other, is one which may well be questioned. In 8–9 cm. Hags he finds the abdominal folds only faintly defined.

The mucous epithelium of the abdominal gut is entirely different from that of the pharyngeal gut. It is single-layered, and there are no traces of the glassy and granular mucous cells. There are, however, numerous highly granular unicellular gland cells, which are highly eosinophilous. The free border of the epithelium is striated; and nearer the lumen end of the cells, *i.e.* outside the nuclear zone, there are many diffuse mitoses. The mucosa is pitted, and is very easily detached from the submucosa owing to the extensive lymph sinus between the two layers. Both MAAS and SCHREINER describe a slender basement membrane which I have not found. It is possible they may be referring to a membrane between the mucosa and the stratum compactum, and which appears to me to belong to the latter layer.

There is no muscularis mucosæ, but in its place MAAS describes what he calls the peculiar and characteristic stratum compactum, which is highly vascular, and dispatches supporting processes into the adjacent lymphoid tissue. MAAS has devoted considerable attention to this tissue, without, however, noticing that it is strictly comparable to the submucosa of the pharyngeal gut. His digestion experiments establish that it is not one of the elastic connective tissues, and he holds that the connective-tissue framework of the abdominal gut is more specialised than that of the pharyngeal gut, since the embryonic formative cells have more and more receded in favour of the cell product. The obvious and important blood sinus which is seen in the stratum compactum immediately under the mucosa is usually flushed with blood, and has a definite lining with longish flattened nuclei. MAAS was unable to find this lining.

External to the stratum compactum is the lymphoid portion of the submucosa, and then follow the weak circular unstriated musculature (no longitudinal musculature) and the serosa with its attached connective tissue.

The lymphoid submucosa is very vascular, and is continued into the folds of the mucosa. Its characteristic feature is the presence of packets of lymph cells associated with the factors of the portal vein, but not with the arteries. Such lymphoid tissue in the wall of the gut occurs in a very few forms (*e.g.*, *Protopterus*), and MAAS regards it as a diffuse spleen, holding that the compact spleen of the higher forms has been produced first by the concentration of such a tissue, and then by its emergence from the wall of the gut. MAAS, who overlooked the essentially adipose nature of the lymphoid zone, observed by SCHREINER shortly before, states that the lymphoid heaps only occur in the more peripheral regions, and then specially round the smaller veins.

On the other hand, I find them in all parts of the layer, and round veins of all sizes. They form a kind of pulp compared by MAAS with the splenic tissue of higher vertebrates. He states that the lymphoid cells resemble the free colourless corpuscles of the blood, to which they undoubtedly give rise: not, however, to the red corpuscles, which always lie free in the vessels and lacunæ, and the early stages of which are never found in the connective-tissue framework of the gut. On the other hand, the early stages of the leucocytes occur in the framework, and the lymphoid tissue of the gut represents their principal source, the associated veins always containing an excess of leucocytes. It is, however, difficult to believe that the lymphoid tissue performs this function only. It is so extensive a structure that some further explanation of its presence must be sought.

SCHREINER describes mitoses both in the epithelial and glandular cells of the abdominal mucosa. Gland cells are never formed from epithelial cells, but are always derived from pre-existing gland cells. The nucleus migrates towards the lumen before it divides, and this explains why the mitoses are always found outside the nuclear zone. SCHREINER finds the lumen end of the cell rich in fat droplets, which diminish when the animal has been kept in an aquarium some days without food. This part of the cell gives the slime reaction with appropriate stains. I agree with SCHREINER that the thick free edging is in two parts—a proximal, binding the cells together; and a striated distal, of elements corresponding to the individual cells.

Both MAAS and SCHREINER state that the abdominal gut is uniform in structure from one end to the other. I have carefully explored the entire length of this section of the gut, and agree to the above statement with, however, this proviso: I have generally found that, either immediately or shortly following the bile duct, the lumen of the abdominal gut undergoes expansion—largely owing to the fact that the mucosa is at this point without folds and almost smooth. The entire wall of the gut, in fact, is here very thin. On the other hand, the above features are not associated with any histological peculiarity. Nevertheless, this region must have some significance. Further, at the hind end of the abdominal gut, the mucosa is thrown into numerous secondary folds, *in which the submucosa takes no part.*

Such are the characters of the two types of gut structure found in *Myxine*. We may now consider the various stretches of the gut in more detail.

MAAS distinguishes the following regions in the gut of *Myxine*, apart from the mouth:—

1. Branchial gut—up to the opening of the ductus œsophago-cutaneus	30
2. True œsophagus—up to the entrance of the gut into the body cavity	3·5
3. Stomach—up to the opening of the bile duct	2·5
4. Mid-gut or abdominal gut	60·5
5. Hind-gut	3·5
	100 *

* These figures are not MAAS', but are calculated from data given by him.

It will be noticed that MAAS does not regard what I have termed the pharyngeal gut as the œsophagus, and in this I entirely agree with him. There is something to be said in favour of considering that portion of the gut extending from the ductus œsophago-cutaneus up to the entry of the gut into the abdominal cavity as the *true morphological œsophagus.* MAAS' description of the region, however, does not always agree with what I have found. He describes regular folds, the interior of which is filled with adenoid lacunar connective tissue. I find the folds anteriorly are twice as high as those of the branchial gut, and higher still behind. Their submucosa is very dense and fibrous, and not different from that of the branchial gut. As regards the epithelium, he says it is layered, but with not so many layers as in the branchial gut; is in two divisions corresponding to the stratum corneum and stratum Malpighi (the nuclei being different in these two layers); and that there is a striking diminution in the slime cells. In my preparations there are more layers in the epithelium of the "true œsophagus" than in the branchial gut, and MAAS' statement only applies to the posterior end. I cannot distinguish the two layers, nor in fact any essential difference between the epithelium of the œsophagus and the branchial gut, in both of which the glassy and granular mucous cells are very abundant. Posteriorly, however, the granular cells are greatly reduced in number, although the glassy cells are still present in quantity. The superficial cells here give the mucin reaction, and the epithelium is more like that figured by MAAS. I find no trace of the muscularis mucosæ described by MAAS, but the unstriped circular musculature is very well marked. MAAS' striped musculature is, of course, the constrictor cardiæ, and does not belong to the intrinsic musculature of the gut.

I see no grounds for regarding that part of the gut which extends from the entrance of the gut into the body cavity up to the opening of the bile duct as a stomach. The bile duct does not coincide with any change in the structure of the gut, and therefore to use it as a boundary is entirely arbitrary. MAAS gives the characters of this part of the gut as follows: Epithelium single-layered, with striated border and no pits. Gland cells and mitoses present, also a muscularis mucosæ. Adenoid submucosa with large vessels. Circular unstriated musculature. In my preparations the striated border and gland cells are not present at the anterior end of the "stomach," but epithelial pits do occur in this region of the gut. I find no muscularis mucosæ, and the submucosa in every sense connects up the dense fibrous submucosa of the œsophagus with the stratum compactum of the abdominal gut.

SCHREINER divides the gut of *Myxine* into a mouth, œsophagus [pharyngeal gut], intermediate region (no stomach), true gut, and ectodermal anus and cloaca. In the mouth he finds the epithelium many-layered, the superficial layer giving the slime reaction, and the basal cells being small and polygonal. The slime cells, the life of which terminates with the discharge of the slime, are exactly similar to those of the skin, and develop in the same way. There are no granular cells. The boundary between the mouth and "œsophagus" is the naso-pharyngeal opening. In the "inter-

mediate region," which may be entirely closed by the constrictor muscle [constrictor cardiæ], the granular cells become rare and finally disappear, the slime cells are reduced in number, and the superficial cells again give the slime reaction as in the mouth.

HAACK, who appears to be unaware of MAAS' paper on the gut of *Myxine*, states correctly that the multicellular oral gland of the lamprey is not present in *Myxine*. He criticises SCHREINER'S paper as regards some of the smaller detail, and finds no transverse folds in the pharyngeal gut, as I do. He regards the gut up to the beginning of the gills as corresponding to the pharynx of *Petromyzon*. My preparations agree with his in one respect—that the granular cells do not contain a continuous thread, as described by SCHREINER. They do not, however, always contain the thread in the outer skin. He compares the granular cells with the gland cells in the œsophagus of the Ammocœte.

The *nasal tube* is surrounded more or less by an extensive lymphatic sinus situated between the nasal rings and the tube itself. The epithelium is many-layered and rests on a distinct basement membrane. Under that there is a dense fibrous vascular connective tissue which diminishes posteriorly. The superficial cells of the epithelium give the mucin reaction. The glassy mucous cells are very numerous and larger than those in the skin, but the granular cells are scarce and quite small.

There are no mucous cells in the olfactory laminæ of the nose, although they are still present in the ventral non-olfactory portion of the tube, the epithelium of which is so thin that the mucous cells not only occupy its entire height, but project beyond it into the lumen of the nasal chamber.

In the *naso-pharyngeal tube* the epithelium is very thin but many-layered, and there is a definite basement membrane. The glassy mucous cells are very numerous, but only a few of the superficial cells give the mucin reaction. The discharging glassy cells project markedly into the lumen of the tube, and often at the other end rest on the basement membrane. There are numerous granular cells in the posterior section of the tube, especially in the region of its opening. Next the epithelium is some very loose vascular connective tissue, which posteriorly becomes fibrous, and then follows the lymph sinus.

The epithelium of the *mouth* near the opening is many-layered, and rests on a dense fibrous connective tissue. There is no differentiated free border. The three or four superficial layers of cells give the mucin reaction, and their nuclei are pushed to one end of the cell. The glassy mucous cells are numerous and large, but there are no granular cells, nor any multicellular glands. There are no mucous cells in the immediate neighbourhood of the teeth, and in fact the number of these cells is reduced in this region, the lateral epithelium further being here very thin, but containing mucous cells.

At about the region where the naso-pharyngeal tube opens into the mouth, *i.e.* opposite the anterior extremity of the notochcord (cp. fig. 1), large numbers of the *granular* mucous cells appear in the epithelium, similar to those in the skin, but

smaller. They also occur in the hinder extremity of the naso-pharyngeal duct. At the same time the glassy mucous cells increase in number, and the superficial cells giving the mucin reaction so characteristic of the anterior section of the mouth almost disappear, to be replaced by an epithelial mosaic. Further back, however, they become more numerous again, but are never as well developed as in the mouth. There is no doubt that we have here a distinct change in the character of the epithelium, which corresponds to the boundary between the stomodæum and the mesenteron.

The submucosa is a very dense fibrous connective tissue immediately under the epithelium, but becomes looser further away from it. The gut behind the velum resembles the velar gut.

Posterior to the velum the gut gradually narrows down to rather more than half the width at the velum, and the lumen becomes correspondingly contracted and flattened dorso-ventrally. It then gradually increases in calibre, the lumen becoming larger and oval in transverse section. These changes, however, involve no corresponding histological change.

There is no real distinction between the pre-branchial and the branchial gut, but the branchial submucosa is more vascular and not so dense, and there are rather more unstriped circular muscle fibres, although they are still very sparse. Again, near the hind end of the branchial gut I have observed a slight tendency for the unstriated musculature to be directed into the *folds*. Both the glassy and, to a lesser extent the granular, mucous cells, are still present in great abundance, but the unstriped musculature embedded in the submucosa almost disappears posteriorly, and external to the submucosa for a short distance we have a new layer, a wide zone of fatty tissue, encircling which is a layer of unstriated muscle. Apart from the epithelium a section of the gut here is not unlike one of the abdominal intestine.

The branchial gut increases gradually in calibre from before backwards, and the lumen is largest a short distance in front of the ductus œsophago-cutaneus. It then narrows down markedly, increases again in the immediate neighbourhood of the ductus, whilst behind the latter, and where it is surrounded by the constrictor cardiæ, it abruptly diminishes, and is smaller and more definite in shape (*i.e.* circular in transverse section) than in any other region of the gut. Behind the constrictor it widens again gradually until the region of the bile duct is reached, and then it rapidly expands into the full size of the abdominal gut.

The transition from the branchial into the abdominal gut may be best studied in a series of longitudinal sections. We then note the following points :—

Epithelium.—No change is noticeable until about the centre of the constrictor cardiæ, where there is a marked diminution in the granular mucous cells. The glassy cells also decrease in number, but not to the same extent. Both kinds of cells, however, may occur right up to the boundary between the two types of gut—*i.e.* between the many-layered and single-layered epithelium. With the diminution of the mucous cells

the superficial cells of the epithelium again assume the mucin-secreting character as in the mouth. The epithelium gradually decreases in height from 72 μ up to the boundary, where it is only 40–48 μ high. The transition is quite sudden. It does not occur at the same level in all the folds—otherwise a straight line would accurately divide the two types of epithelium. The single-layered epithelium of the abdominal gut is at first without the striated border, nor does it possess any gland cells. It very gradually increases in height, and acquires first the striated border and then its characteristic unicellular glands.

Submucosa.—Dense and fibrous in the branchial gut, but immediately in front of the constrictor cardiæ it is largely replaced by a thick layer of fatty areloar tissue. In the region of the constrictor, however, the submucosa is again, and even more, dense and fibrous, and becomes increasingly so as it passes backwards. Behind the constrictor (*i.e.* at the epithelial change) it gradually diminishes, and passes without a break into the stratum compactum of the abdominal gut. There is no doubt that the latter layer is only another form of the same tissue as the submucosa of the pharyngeal gut, although its staining reactions are slightly different. The curious submucous blood sinus associated with the stratum compactum may be traced as far forwards as the epithelial change.

Musculature.—The unstriated musculature gradually increases as we trace the branchial gut backwards, and it is a very conspicuous layer in the fatty region immediately in front of the constrictor cardiæ. It diminishes somewhat at the anterior end of the constrictor, but increases again as it passes backwards, decreasing once more at the epithelial change, finally becoming directly continuous with the weak unstriated musculature of the abdominal gut. The new layer, therefore, in the latter gut, which is not represented in the branchial gut, is the thick zone of fatty lymphatic tissue between the stratum compactum and the unstriated musculature.

The entrance of the bile duct marks no change in the character of the gut, and hence I am unable to agree with MAAS that there is a representative of the stomach in *Myxine*. The epithelium, stratum compactum, and the lymphoid tissue are the same both in front of and behind the aperture of the bile duct, although the typical abdominal gut extends only a very short distance in front of this point.

The passage of the mid- or abdominal gut into the hind-gut or cloaca is also best observed in serial longitudinal sections. We thus find:—

Epithelium.—Insensibly diminishes from 120 μ, losing its gland cells and its striated border, until at the boundary it is only 32–56 μ high. MAAS figures the striated border and the gland cells right up to the change, a condition not found in any of my preparations. The single-layered epithelium of the abdominal gut meets the many-layered epithelium of the cloaca at a bevel joint, dissimilar to the junction of the branchial and abdominal guts, and in such a way as to suggest that the abdominal epithelium represents the gradually heightened superficial layer of cells of the cloacal epithelium. The latter increases slowly in height up to 80 μ, and for some distance

is devoid of the glassy and granular mucous cells. Near the cloacal opening, however, and in the dorsal chamber of the cloaca,* the two latter become extremely numerous—in fact much more so than they are in the neighbouring skin. Posterior to the anus, the lining of the entire cloaca, and even the urinary papilla, contain both kinds of mucous cells.

Submucosa.—The stratum compactum behaves as at the anterior boundary, and passes gradually into the dense and more deeply staining fibrous submucosa of the hind-gut. In the 19-cm. Hag the submucosa of the posterior extremity of the mid-gut is almost replaced by large blood spaces. The characteristic blood sinus in the stratum compactum immediately underneath the mucosa can be traced no further back than the change in the epithelium. The lymphoid cells are not present at the extreme end of the submucosa of the mid-gut, and the adipose areolar section of the submucosa dies away somewhat in front of the epithelial boundary.

Musculature.—In the sections of the 25-cm. Hag a new tissue appears in the hind-gut. The unstriated musculature of the mid-gut disappears, and is replaced by a primitive tissue resembling an extremely simple form of cartilage, unlike, however, any definitive cartilage of *Myxine*. It encircles the whole of the hind-gut, exclusive of the posterior extension of the body cavity and of the segmental ducts, and recalls the thin sheet of cartilage described by AYERS and JACKSON in the wall of the cloaca of *Bdellostoma* (cp. my Part I., p. 786). In the sections of the 19-cm. Hag this tissue is not present, and its place is occupied by a well-developed and undoubted unstriated circular musculature, but there are indications posteriorly of its replacement by the connective tissue.

MAAS failed to find any glassy or granular cells in the cloacal epithelium, although he says they reappear in the "anal" slit itself. He also describes a muscularis mucosæ, a statement I am unable to confirm. SCHREINER, like myself, finds both kinds of mucous cell in the cloaca.

The height of the mucous epithelium in the different regions of the gut may now be given. The measurements are in μ. The nasal tube at the opening is 48; it rises to 100 and sinks to 60 at the posterior end. In the naso-pharyngeal duct the epithelium is only 32 at the anterior end, but it gradually deepens as it approaches its oral aperture, where it is about 80. In the mouth, up to the posterior extremity of the velum, the height varies from 80 to 140, but is more frequently about 100, the lower figure, however, being more usual behind. In the pre-branchial gut the epithelium is very constant, and measures almost invariably 100. In the branchial gut it drops from 100 to 80. It rises in the region of the constrictor cardiæ to 100 and 120, but falls to 80 on the first entry of the gut into the abdominal cœlome. In the abdominal gut the figures vary from 102 to 160, the commonest measurement being 140, whilst at the posterior end it is 120.

* *i.e.* in the region of BURNE's "anal slime gland."

G. The Liver and Biliary Apparatus.

1. *Superficial Anatomy* (Figs. 4 and 13).

The liver consists of two lobes—a large posterior and a smaller anterior. When the body cavity is opened by a median ventral incision the anterior lobe is observed to overlap the posterior, the latter on the left passing forwards under the anterior lobe. On the right the gall bladder projects from a notch between, and dorsal to, the two lobes of the liver, being partially overlapped by both, the right posterior extremity of the one and the anterior extremity of the other being bevelled off to receive it. The anterior border of the anterior lobe is just at the level of the two external branchial openings.

The sub-intestinal vein, formed by factors from the ventral wall of the anterior abdominal gut, suddenly emerges from the gut wall opposite, or in front of, the posterior end of the posterior lobe of the liver, and passes downwards along the hinder vertical border of the hepatic ligament to reach the apex of the posterior lobe. From here it passes forwards towards the sinus venosus along the entire length of the ventral surface of the posterior lobe. A smaller branch, however, may be traced along the dorsal surface. These conditions, or rather their superficial relations, vary in different individuals.

The mesentery, which suspends the gut, passes from the ventral wall of the gut on to the posterior lobe of the liver as the hepatic ligament. It supports the posterior lobe along its whole length, the only interruption being in the region of the gall bladder.

The depression associated with the point of exit and entry of the posterior hepatic duct and vessels is situated in the direct plane of the hepatic ligament. Hence the two factors of the ligament, in passing straight on to the liver at this place, simply diverge to allow the passage of the vessels. In front and on the right, the posterior lobe of the liver is bevelled off dorsally to receive the gall bladder, whilst its anterior extremity is overlapped ventrally by the anterior lobe. The two lobes are absolutely distinct, each having its own independent serosa.*

In the region of the gall bladder the mesentery passes loosely from the gut on to the right side of the gall bladder. This admits the passage of the various ducts and vessels associated with the gall bladder and the two lobes of the liver. From the left side of the gall bladder the mesentery is reflected on to the dorsal surface of that portion of the posterior lobe of the liver in front of the depression mentioned above.

Unlike the posterior lobe, the anterior lobe of the liver has no definite ligament, but its posterior edge usually more or less adheres to the posterior lobe. The mesentery passes on to it from the anterior left surface of the gall bladder, and reaches it immedi-

* This statement must be qualified. In one series of sections I found a slight but quite unmistakable fusion of the glandular tissue of the mesial edge of the posterior lobe and the dorsal surface of the anterior lobe in the region of the overlap a little to the left of the middle line of the body. Further, in one dissection the two lobes of the liver were completely fused into one body.

ately behind the region where its vessels enter and leave. From here it extends backwards, forming a separate bag in which the anterior lobe lies, and its only attachment is in front where the mesentery passes from almost the entire anterior edge of the lobe on to the pericardio-peritoneal partition, itself in its free portion consisting of a double sheet, *i.e.* a peritoneal and a pericardial factor. Elsewhere it is the latter factor which excludes the liver from the pericardial cavity.

On the side of the intestine and the body wall the posterior lobe of the liver bears a prominent anterior obliquely curved bevel for the reception of the gall bladder.

When the lobes of the liver are turned over to the left and pinned down so as to expose the whole of the gall bladder, the latter is seen to be a relatively very large sac. It is dorsal to the liver, and entirely on the right side of the body. Two of its ducts are seen at once (*a.h.d.* and *p.h.d.*). They are the two hepatic ducts—really hepato-cystic ducts—arising one from each lobe of the liver (*a.l.l.* and *p.l.l.*), from its dorsal surface in the middle line, respectively a little in front and a little behind the gall bladder itself (*g.b.*). Between these two the bile duct (*b.d.*) leaves the ventro-mesial surface of the gall bladder, and, passing somewhat forwards, soon enters the gut a little to the left of the mid-ventral line and a short distance behind the heart. If the intestine be split up, the bile duct is observed to open into it by a conspicuous aperture at the apex by a large backwardly directed papilla. As the bile duct approaches the intestine its wall becomes thickened—due to an aggregation under the serosa of the follicles of the supposed "pancreas," the structure of which is described elsewhere.

On opening the gall bladder, and delicately brushing its internal surface clean, we observe a conspicuous depression, with an aperture at the bottom, on the surface facing the intestine. This is the opening of the bile duct. A short distance in front, but to one side of it, is the smaller and less obvious aperture of the anterior hepatic duct. A slight distance behind and also to one, and the opposite, side (*cp.* fig. 4) is another similar opening—that of the posterior hepatic duct. There are thus three openings into the gall bladder, and the hepatic ducts have no direct connection whatever with the bile duct. In one specimen I found two anterior hepatic ducts, each having a separate opening into the gall bladder, there being therefore in this case four cystic openings. The additional duct, which was very small, was formed by the fusion of two thread-like tubes from the anterior lobe of the liver, but on nearing the gall bladder it became enlarged to the normal width and opened by a small aperture close to the larger one of the normal duct.

The anterior hepatic duct (*a.h.d.*) courses almost straight backwards, until it reaches the gall bladder, where it bends abruptly on itself in a U and opens almost at once into the cyst. The posterior hepatic duct (*p.h.d.*) passes almost straight forwards, but on reaching the gall bladder it bends over to the opposite side (*cp.* fig. 4), almost at a right angle, to reach its aperture. This difference between the courses of the two hepatic ducts I find also in the sections. As shown in fig. 4, each hepatic duct is accompanied by a branch of the common portal vein (*c.p.v.*) and of the cœliac

artery (*cœ.a.*), the latter especially being closely attached to the duct, and somewhat difficult to separate out. All three respectively enter and emerge for the liver at the same place. The branch of the cœliac artery, dividing into the cystic and hepatic arteries, closely accompanies the bile duct—in this case anteriorly. The main stem of the artery courses along the intestine, and may pass over or under the root of the bile duct. In another, and well-injected, specimen the cœliac artery behaved as follows: it arose as a *paired* artery, which, after giving off on each side various branches, *e.g.*, to the pronephros, fused ventrally so as to form a complete ring around the gut in front of the bile duct. From this ring another and smaller circle was given off below the gut which surrounded the bile duct. From the latter arose the branches to the "pancreatic" follicles, the bile duct and gall bladder, and the anterior lobe of the liver. Posteriorly the lesser ring gave off a large branch to the mid-ventral surface of the gut, and the branch to the posterior lobe of the liver.

In a *Bdellostoma cirrhata*, Sch., dissected by Dr DAKIN, the anatomy of the gall bladder and cystic ducts was found to be essentially the same as in *Myxine*.

J. MÜLLER's figure of the gall bladder and ducts may conceivably represent one of the variations which are so common in *Myxine*, but it is certainly quite inaccurate as a representation of the normal condition. He figures the two hepatic ducts opening into the base of the bile duct. His very brief reference to this region in the text takes no account of the openings of the ducts. The fact that the hepatic ducts may open direct into the gall bladder is, of course, an unusual but not a unique phenomenon. It was, I believe, first described in the ox by VERHEYEN in 1710, and occurs as a rare variation even in man. I am not aware, however, of any case so clear and interesting as that of *Myxine*.

WIEDERSHEIM, in the first edition of his *Lehrbuch* (Th. ii. p. 590), publishes an original figure of the biliary apparatus of the Myxinoids, which agrees practically with MÜLLER's figure, and to which therefore the comment above also applies. His remarks are, however, more definite. He says: "Aus jedem Leberlappen tritt ein *Ductus hepaticus* hervor und diese confluiren zu einem *Ductus choledochus*, in dessen Rückwärtsverlängerung die *Vesica fellea* (resp. der Ductus cysticus) gelegen ist."

Even MAAS, in his work on the "pancreas" of the Myxinoids, agrees practically with MÜLLER and WIEDERSHEIM. In *Myxine* he says (p. 3): "Die Beziehungen der drei Gänge sind so innige, dass zwischen vorderem Lebergang und der Austrittsstelle des Gallenganges nur ein verschwindendes Stück Gallenblasenwandung liegt, und dass für den hinteren Lebergang der Gallengang einfach die Fortsetzung bildet." In *Bdellostoma* he is more definite (p. 571): "Dieser letztere [bile duct] setzt sich, durch einen sehr kurzen Ductus cysticus mit der Gallenblase in Communication stehend, aus der Verbindung von rechtem und linkem Lebergang zusammen und mündet wie bei Myxine genau ventral median in den Darm ein." I have repeated my dissections of the biliary apparatus of *Myxine* a number of times, and find on the whole a remarkable agreement with the conditions already described. The only variation of importance was

the occurrence of the extra anterior hepatic duct mentioned above. If the gall bladder is split open, and its internal surface carefully examined, there is no difficulty in finding the three perfectly distinct apertures as I have described them.

2. *General Anatomy of the Liver.*

(A.) First, as regards the blood-vessels and hepatic ducts. The *sub-intestinal vein*, on reaching the posterior extremity of the posterior lobe of the liver, behaved in one case as follows: it split into two large vessels—one passing on to the ventral convex surface of the lobe, and the other on to the dorsal concave surface. The latter itself split into two almost equally sized vessels, and both, after repeated branching, were finally dissolved among the liver tubules. This proves that the sub-intestinal vein acts not only as a collector but as a distributor, *i.e.* that it brings blood to the liver just as the portal vein does.

On the other hand, the vessel on the convex ventral surface, which represents the main trunk of the sub-intestinal vein, remained fairly constant in size in spite of frequent interchange of vessels with the liver. Large veins were undoubtedly received, showing that the sub-intestinal collects blood returning from the liver, and is therefore the *posterior hepatic vein*. Its course is always more or less superficial.

No factors of the hepatic duct are associated with the sub-intestinal vein or its constituents.

Anteriorly the sub-intestinal comes more to the surface of the lobe, and is plainly visible in a surface view. It leaves the posterior lobe at its extreme anterior point as its sole or principal hepatic vein and opens into the sinus venosus. There may, however, in addition, be another efferent vessel associated with the posterior lobe, opening separately into the sinus venosus and corresponding to the similar vessel (*anterior hepatic vein*) draining the anterior lobe of the liver. It may be called the *accessory posterior hepatic vein*, and, like the sub-intestinal, it receives blood from the irregular spaces everywhere present between the liver tubules, and courses along the *dorsal* surface of the lobe. I thought at first that this vessel might be the direct continuation of one of the dorsal branches of the sub-intestinal described above, just as the sub-intestinal itself is continued forwards as the principal hepatic vein of the posterior lobe, but the specimens I investigated with respect to this point gave no support to such a supposition. The accessory posterior hepatic vein, therefore, is a true hepatic vein, and is actually constituted within the substance of the posterior lobe of the liver.

From behind forwards the above vessels open into the sinus venosus in the following order: (1) accessory posterior hepatic vein; (2 and 3) posterior hepatic or sub-intestinal vein and anterior hepatic vein almost simultaneously. In front of this region the sinus venosus in my large series of sections received seven independent smallish *accessory anterior hepatic veins* from the anterior lobe of the liver, which extended forwards for some little distance in front of the place where the main anterior hepatic vein left it.

There is a distinct difference between the larger branches of the portal vein and those of the sub-intestinal vein. In the former case they have an obvious connective-tissue sheath, and are surrounded by factors of the hepatic duct, whilst in the latter case they are irregular spaces between the liver tubules, apparently unlined,* and usually contain a lesser quantity of blood. Nevertheless, the two series of spaces communicate freely within the liver. A forward injection of the portal vein at once passes from the liver substance backwards along the sub-intestinal vein.

The *portal vein*, on entering the liver, splits into a number of large vessels of considerable blood capacity compared with that of the vein itself. The pressure of blood in the liver, therefore, must be low.

As that division of the portal vein which enters the posterior lobe of the liver is coursing backwards over the surface of the liver preparatory to plunging into it, there is given off first a large vessel which courses forwards in the interior of the anterior section of the lobe, and which preserves its identity almost up to the anterior extremity of the latter. The portal vein then detaches another large vessel, which supplies the more central section of the gland. Finally, it enters the lobe at the point where the hepatic duct leaves it, coursing at first alongside and external to the associated larger factors of the hepatic duct near the surface of the lobe, and giving off large vessels to the interior. It then penetrates to about the centre of the lobe, still accompanying the larger factors of the hepatic duct. Finally, as the posterior extremity of the lobe is approached, and the hepatic duct is represented by a large number of very small tubules, the portal vein splits first into two and then into four, and so on until its identity is no longer maintained.

With regard to the anterior division of the portal vein to the anterior lobe of the liver, the vessel, on entering the lobe, gives off two large branches which pass backwards, and supply that part of the gland behind the point of exit of the hepatic duct. The remainder passes forwards, accompanied by the factors of the hepatic duct, soon splits into two and then into four, and thereafter behaves in the same way as in the case of the posterior division.

Near the point of exit from the liver we encounter the usual portal canals, consisting of one or more branches of the portal vein, hepatic artery, and hepatic duct, enclosed in the connective-tissue sheath of Francis Glisson. This association, however, has by no means the definite significance and regularity of the higher animal. The artery is distinguished by a well-defined lining and its conspicuous closely set nuclei projecting into the cavity of the vessel.

The *posterior hepatic duct*, after leaving its lobe of the liver, receives a large duct from the anterior section of the lobe. If this itself be now traced forwards, it almost at once, and before becoming actually buried among the liver tubules, splits into a very large number of small ducts which are arranged round the portal vein and its

* The boundaries exhibit a few flattened nuclei at intervals which belong to the inconspicuous lining of the vascular space and not to the basement membrane of the tubules.

branches. These ducts are readily identified by their more deeply staining shallow epithelium and closely crowded nuclei.* The contrasted liver tubules, of course, open into them.

The main or posterior section of the posterior hepatic duct, on being followed backwards from its point of exit from the liver, is found to behave in precisely the same way as the smaller anterior section. Whenever the portal vein gives off a large branch, the hepatic duct detaches a corresponding branch, and this immediately breaks up into a large number of small tubules which at once surround the vein. There is, however, one difference between the two sections of the posterior hepatic duct. The posterior one preserves its identity for some distance within the liver—in fact, as long as the portal vein is represented by a conspicuous vessel. But when the latter splits into two, the hepatic duct is thereupon dissolved into numerous small tubules.

In places the biliary tubules become enlarged, and here contain a substance which looks very like broken-down blood corpuscles. It is possible this may be a pathological manifestation.

The *anterior hepatic duct* leaves the anterior lobe of the liver as two large tubes which, however, immediately join. Each is formed by the junction of two ducts—in one case of two relatively small ducts. These then enter the liver in company with the portal vein. Since the greater part of the lobe lies anterior to the exit of the hepatic duct there is not the same occasion, as in the case of the posterior lobe, for the existence of anterior and posterior sections of the duct, and, as a matter of fact, the two tubes mentioned above are concerned mostly with that part of the lobe anterior to the point of exit. A few smaller tubes pass backwards to drain that part of the lobe posterior to the exit place. The factors of the anterior hepatic duct behave, and are related to the anterior branch of the common portal vein, exactly as in the case of the posterior lobe already described.

The liver is extremely vascular. It contains large, sometimes very large, irregular blood sinuses, only partially filled with blood, which at first sight appear to have no definite walls. As above stated, other blood spaces have an obvious connective-tissue wall. The former are associated with the sub-intestinal and hepatic veins, the latter with the portal vein. In serial sections I have been able to trace a direct continuity between these two types of spaces.

In a well-injected liver each tubule is seen to be completely surrounded by a vascular space—in fact so much so that the substance of the liver appears to include more blood tissue than liver tubules. None the less, I have found no clear case of a vessel entering a tubule—they remain always outside them. There are no intercellular or intra-tubular vessels.

Injection from the heart (*i.e.*, *via* the hepatic arteries) or from the portal vein gives the same result. A coarse vascular network is disclosed which penetrates everywhere between the liver tubules, and constitutes not a capillary system but a *reticular sinus*.

* In one case I found only three cells in transverse section.

This sinus is usually injected if the needle of the syringe is simply plunged into the liver at random. The liver admits of considerable vascular distension. The tubules may be so close together as to obliterate, or almost obliterate, the intervening blood spaces, or the latter, if congested, force the tubules apart and form relatively large channels.

(B.) Second, as regards the histology of the liver tubules. The Myxinoid liver is a simple tubular or racemose gland, in which the tubules end blindly and form no networks. Microscopically there is only one kind of tubule. I have searched in vain in my serial sections for any glandular tissue which might constitute a histological pancreas. The liver is enclosed in the usual serous and fibrous coats, the latter with long nuclei; but no trabeculæ are dispatched internally to ramify among the liver tubules. In fact, the liver has only an extremely slight connective-tissue framework. Some of the large superficial blood-vessels, however, are invested by fibrous tissue continuous with that of the external fibrous coat.

The liver tubules are circular or oval in transverse section, and possess a very thin non-cellular basement membrane. The central cavity, varying with the state of activity of the tubule, may be large and irregular, small and round, or apparently wanting altogether. Under the highest magnification the free border has a well-defined margin outlined by chromophilous granules like exceedingly minute nuclei. The diameter of the tubules varies from 32 to 78 μ—average 56 μ; height of the cells from 8 to 28 μ—average 17 μ;* diameter of the cavity from 4 to 44 μ (Holm gives 3 to 8 μ); the number of cells seen in a transverse section of a tubule is from 4 to 15, average number 8 to 9 (Braus says 4 to 6 and Holm 5 to 10).

The cytoplasm of the liver cells may be very vacuolated. Large intracellular cavities may occur which themselves open into the larger lumina of the tubules. Intercellular canaliculi or bile capillaries may be very numerous and striking, so that in transverse section a star-shaped cavity is seen. The cells of the whole liver may be thus vacuolated, but here and there small aggregations of tubules are found with solid cytoplasm and slightly larger nuclei. These are in sharp contrast with the surrounding vacuolated cells, owing to their naturally taking on a deeper stain.

Small patches of adipose tissue are to be seen scattered among the liver tubules.

The nuclei of the liver cells are spherical, with well-marked reticular chromatin, and are obvious differentially staining nucleolus. They measure from 5 to 10 μ, but the larger sizes are the more frequent. Occasional mitoses, of the type described by the Schreiners in other *Myxine* tissues, may be observed.

In thick sections we notice that the superficial tubules are looser, have larger cavities and more vacuolated cytoplasm, and are not so packed together as are the more central tubules.

The structure of the liver of *Myxine* has been investigated by Braus, who used

* According to Braus, 30 μ.

material down to 7 cm. in length. He describes cytozonal networks formed by the bile channel splitting, surrounding little islands of several cells, and then joining up again. I also find these. BRAUS confirms RETZIUS that the innumerable small blind side capillaries given off from the central lumen of the tubule, which penetrate between the liver cells, do not reach the periphery of the tubule. This is generally, but not universally, true. He also states that, besides the nucleus, the body of the cells contains large "nebenkerne" resembling corresponding structures in pancreatic tissue. He believes these to be the remains of the achromatic spindle of recent mitoses, and thus archoplasmic in character. Whilst agreeing that the liver of *Myxine* is a tubular gland, he describes certain deviations from the purely tubular structure which suggest the origin of networks of bile capillaries.

HOLM states that the liver of *Myxine* is a typical tubular gland. He describes a strong layer of unstriated muscle fibres round the larger blood-vessels which I have not found, and asserts that the blind intercellular bile capillaries reach the periphery of the tubule. He has injected the liver from the portal vein.

3. *Bio-chemistry of the Liver.*

I have not found it possible to overcome satisfactorily the practical difficulties in the way of testing the secretion of the so-called "pancreas" of *Myxine*. The gland itself is so very small that almost hundreds of dissections would be necessary, and its situation is such that one could never guarantee any extract made from them would be free from the secretion of the liver. In any case, however, this does not matter. As far as my material is concerned, the "pancreas" can have no effect on proteid digestion in the animal.

An effective pancreas, therefore, being absent, the question is raised as to the function of the liver. Two problems had to be solved: (1) Was the liver a true liver—could it be compared with the liver of higher vertebrates? (2) Was it more than a liver —*i.e.* was it also a digestive gland? To the former point an answer in the affirmative can be given. I had hoped to have included here an account of the digestion experiments which have been carried out on the liver and gut of *Myxine*. These, however, are not yet complete, and cannot now be completed until next year. The Hags migrate into deeper water in the winter, and at the time of writing (September 23) the females have already left, only one out of the 150 examined being a female.

The chemical and physical properties of the contents of the gall bladder were investigated in several freshly killed *Myxine*. I ought to add that these specimens had been kept in the tanks at Cullercoats for some time, and it is well known that *Myxine* do not maintain their health in captivity, nor will they feed. The following results might hence have to be slightly modified if bile taken from animals fresh from the sea were examined. Exactly similar experiments were carried out with a specimen of bile taken from a freshly killed ox, the two series of observations being performed side by side.

A careful comparison of the results obtained shows that *Myxine* bile, although obviously differing in percentage composition, contains all the essential constituents of ox bile, and hence the liver of *Myxine* is a true vertebrate liver, whatever else it may be.

Both fluids have a greenish brown colour, but whilst ox bile is a clear viscous fluid, *Myxine* bile is almost opaque. The latter, however, is of a much more watery consistency, due to the presence of a smaller percentage of mucin. *Myxine* bile has the characteristic bitter taste of ox bile, but the latter is more aromatic. Further, ox bile is slightly alkaline to litmus paper, but *Myxine* bile is neutral.

The presence of mucin and nucleo-protein may be tested for by adding a few drops of acetic acid to a small quantity of bile, when a precipitate insoluble in excess of acid is thrown down. Ox bile gave a bulky mucinoid precipitate with this test, but with *Myxine* bile the precipitate was only sufficient to render the fluid turbid. With methylated spirit both fluids gave a bulky precipitate of mucinoid nucleo-albumin coloured by pigment.

The pigment tests were not, on the whole, quite so pronounced as with ox bile, but were sufficiently good to leave no doubt as to the presence of bile pigments in *Myxine* gall.

On shaking up a small quantity of ether with the two separate samples of bile, no pigment was extracted by the ether, but, on the addition of a few drops of concentrated hydrochloric acid, nucleo-protein was in both cases precipitated and pigment extracted by the ether. Ox bile gave much the better result, both in the amount of the precipitate and of the pigment extracted. Pigment was further tested for by GMELIN'S ring test. This is carried out by saturating a portion of filter paper with bile, and placing a drop of fuming nitric acid in the centre of the saturated area. After a short time a number of differently coloured concentric rings appear at the margin of the nitric acid drop, and slowly spread. The order of the colours is (1) yellow, appearing at the junction of bile and acid and due to the pigment choletelin; (2) red; (3) violet, passing into blue, due to bilicyanin; and (4) green, due to biliverdin. Owing to the limited quantity of *Myxine* bile available, only a very small area of the filter paper could be saturated, but rings of yellow, red, and blue could be faintly seen. Ox bile, again, gave the more striking result.

As regards bile salts PETTENKOFER'S test gave an excellent result with *Myxine* bile. The test consists in adding a drop of 10 per cent. solution of cane sugar to a few drops of bile, and thoroughly shaking. Concentrated sulphuric acid is then carefully poured down the side of the tube, and at the junction of the two liquids a purple ring slowly develops. On shaking, the contents of the tube are coloured a deep purple. By using a solution of cane sugar and sulphuric acid only, by way of control, no purple colour was produced, but only the characteristic brown colour due to the charring of the sugar by the sulphuric acid. Hay's test depends on the presence of bile salts reducing the surface tension of that liquid. When flowers of sulphur are placed on the surface of bile they slowly sink to the bottom, but with water only the surface tension

is sufficiently high to keep the sulphur at the surface. The rate of fall of the sulphur particles was much more rapid with ox bile, but nevertheless with *Myxine* bile quite a large quantity of the sulphur sank to the bottom of the tube.

Since the above was written, Professor MEEK obtained a fresh supply of *Myxine*, and I at once went to Cullercoats and collected the bile from about 100 specimens. I find the best way to do this is to remove the two lobes of the liver separately, and then detach the gall bladder from the gut. Severing the hepatic ducts and the bile duct does not cause bile to escape from the cyst. The latter can then be washed free of blood, and slit open inside a test-tube. All the bile is thus collected without any admixture of blood. It varies greatly in colour from a pale yellow to a deep green. The colour of the liver also varies considerably.

The fresh bile is rather more gelatinous than that taken from animals kept for some time in the laboratory tanks, and consequently the precipitate of nucleo-protein obtained by acidifying the bile with acetic acid is much more pronounced. In the ether and hydrochloric acid test a much greater proportion of pigment was extracted by the use of dilute acid.

GMELIN'S ring test was more successful with the fresh bile. This is better carried out by pouring a thin film of bile on to a clean porcelain tile, and then adding the acid. The rings visible were a very faint yellow, red, violet passing into blue, and a very faint green. The red and blue zones were the most predominant, and this suggests that bilicyanin is in excess of the other pigments.

4. *Histology of the Gall Bladder.*

The gall bladder is lined by a single layer of epithelium. The cells are tall and narrow, and may measure as much as 35 μ by 3 μ. The nucleus is at the base and the chromatic material very concentrated, so that the nucleus stains a solid black with iron hæmatoxylin. The free border of the cells, looking like a string of beads, is denser than the remainder, and readily strips off in imperfectly preserved material, or the free surface may dispatch into the lumen of the gall bladder innumerable sessile droplets. The cells are not in apparent contact, but are separated by a narrow non-staining zone. In badly preserved material the cells shrink considerably, and are then separated by intervals wide enough to be distinguishable under the low power of the microscope. The cytoplasm of the cells is coarsely vacuolated.

Immediately investing the lining epithelium is a complex fibrous coat. This is essentially the vascular investment of the gall bladder, which, as shown by injections, is richly vascular with a well-developed capillary system. Arteries and veins and their connecting capillaries are readily distinguishable. Blood-vessels are very numerous just under the epithelium, although in nearly all cases a few fibres intervene between the vessels and the base of the epithelial cells. I have, however, here and there seen fine vessels penetrate between the lining cells themselves.

The fibrous coat falls readily into three layers—a central transverse one and an

outer and inner coat in which the course of the fibres is predominantly longitudinal. The central coat has a specific staining reaction, and in general appearance differs from the other two coats, its nuclei being far more numerous and up to 30 μ long, and its fibres more accurately parallel. It does not appear in all cases to run continuously round the gall bladder, but is interrupted at intervals. It is the only one of the three coats which is distinctly muscular, the other two being composed of connective-tissue fibres. The inner coat is the most vascular. The connective-tissue fibres have shorter and more irregular nuclei, and have a coarse, granular, wavy appearance. In some methyl-blue-eosin preparations the connective-tissue nuclei stain blue, and the nuclei of the muscular layer red. In other cases the order of the layers appears to be reversed —the outer layers being muscular and the central one connective-tissue, and the conditions may even vary in different regions of the same gall bladder.

A number of measurements of the thickness of the various coats of the gall bladder results in the following average :—epithelium, 26 μ ; inner fibrous coat, 29 μ ; middle coat, 16 μ ; outer coat (very variable), 41 μ ; total thickness of the gall bladder, 112 μ. These measurements apply to the right lateral free surface of the gall bladder. On the left the outer coat passes externally into a very loose connective-tissue layer transmitting the larger blood-vessels.

Maas has a few notes on the histology of the gall bladder in his work on the "pancreas" of *Myxine* (p. 6). He finds in "old specimens and sections in a favourable plane" *two* layers of unstriped muscle—one circular and one longitudinal. The layer he misses is evidently the outer one, which I also have found sometimes represented by a wide zone of very loose connective tissue. His description of the other two as both muscular is doubtless well within the variability of the animal.

5. *Histology of the Hepatic Ducts.*

The hepatic ducts consist of a central single layer of epithelium, without a basement membrane, almost directly under which is a rich vascular network. The epithelium is surrounded by a coat of coarse connective-tissue fibres having an average thickness of 60 μ, and which lodges the nerve bundles. This itself is enclosed by a very loose connective-tissue sheath. When the hepatic duct is cut across a triple lumen is disclosed. The largest is that of the duct itself; the next is one of the two branches of the common portal vein ; and the smallest is a branch of the cœliac artery. In the neighbourhood of the artery and vein is found also an accompanying nerve. Further smaller vessels and nerves are present, as above mentioned.

The hepatic duct is circular in transverse section and measures about 300 μ in diameter in an average specimen. Its lumen is not regular, but is indented here and there. The lining epithelium consists of tall narrow cells about 72 μ high and 4 μ wide. The nuclei are at the base, and are in marked contrast with those of the gall bladder. They are oval and vesicular, with a well-marked nuclear membrane and reticular chromatin. The cytoplasm is granular and may be vacuolated, the cell

outlines are not very clearly defined, and the free border is somewhat modified and tends to flake off into the lumen of the duct. Occasionally an isolated nucleus in mitosis may be seen between the row of basal nuclei and the free border.

The wall of the gall bladder is not perforated by the hepatic ducts at right angles to its surface, but very obliquely, with the result that a flap is formed which acts as a valve to the opening. At this point the transition from the epithelium of the hepatic duct to that of the gall bladder may be well studied. The cells of the duct become shallower and vacuolated, the non-staining areas between the cells appear, the modification of the free border becomes emphasised into the moniliform strip of the gall bladder epithelium, and the clear vesicular nuclei pass into the solid irregular nuclei of the bladder. On the side of the valve the transition from one kind of nucleus to the other is more sudden.

6. *Histology of the Bile Duct.*

The bile duct, like the hepatic ducts, consists of a single layer of irregular epithelium exhibiting numerous mitoses and without a basement membrane, and surrounded by connective-tissue coats. There are, however, some obvious differences. It is, of course, larger, and has a diameter of 525 μ in a moderate-sized specimen outside the region of the "pancreas." The lumen accounts for at most 225 μ of this. The wall is also somewhat thicker than that of the hepatic duct, but, owing to the pitting of the epithelial lining, this varies very greatly. In an average case the epithelium is 105 μ tall, and the connective-tissue coat 75 μ. The bile duct perforates the gall bladder more or less obliquely, but the aperture appears to be permanently and widely open, since I find no signs either of a sphincter or a valve. The transition of the epithelium of the bile duct into that of the gall bladder resembles that elsewhere described in the case of the hepatic ducts.

As the bile duct approaches the gut its wall becomes thickened owing to the presence of the "pancreas," the acini of which are situated within the thickness of the connective-tissue sheath of the bile duct. The latter penetrates the wall of the gut almost at right angles, and has a large opening at the apex of a prominent papilla, the connective-tissue coats being here of greater thickness. At the base of this papilla the lumen narrows down somewhat, but so far I have not found more than a sparse collection of unstriped muscle fibre in connection with the opening into the gut, and in fact there may be only equivocal traces of unstriped muscle in any part of the bile duct. In other examples, however, an unstriped layer immediately external to the epithelium is plainly establishable.

The lumen of the bile duct is not regular, but is thrown into many pits or bags. This is due both to the folding of the epithelium, and also, and rather, to the variability in height of the cells themselves. Many of the pits are long and narrow, as if they were the terminations of glandular ducts; but in nearly all cases they end blindly, in a few cases in an ampulliform enlargement, without reaching the periphery of the

epithelium. Again, narrow duct-like or vesicular cavities appear quite frequently in the epithelium, and terminate blindly in *both* directions. Further, I have seen a duct bent like a U and opening at both ends into the lumen of the bile duct. Again, they appear quite freely in parts of the bile duct outside the region of the supposed pancreas.

The appearance presented by many of the vesicular cavities within the epithelium of the bile duct is that of abortive evaginations. The cavity is surrounded by a layer of non-glandular epithelial cells resembling those of the bile duct epithelium, and it may or may not communicate with the lumen of the bile duct. Such structures are commonly present in the centre of the lobules of the "pancreas." They give to those parts of the bile duct where they occur the appearance of an epithelium of more than one layer, and in any case it is not strictly unilaminar, as, for example, are the hepatic ducts and the mucous membrane of the gut in this region.

The free surface of the epithelium has a sharp cuticular edge, according to MAAS, and flakes off into the cavity of the duct. The cells also extrude a substance which stains black with iron hæmatoxylin. This material may in some cases be seen within the cytoplasm of the epithelium, whilst the lumen of the duct itself is devoid of it.

The nuclei of the epithelium of the bile duct are oval, clear, and vesicular, and exhibit a reticular chromatin sometimes with, but often without, definite nucleoli. The cells themselves have well-defined cell walls.

7. *The "Pancreas."*

In 1896 (37 and 38) MAAS described what he called a pancreas-like organ in *Myxine* and *Bdellostoma.** He found, surrounding a portion of the bile duct, and also partly embedded in the serosa of the gut, and somewhat more strongly developed in older specimens, a peculiar glandular organ which he interprets provisionally as a pancreas. He states that it may be recognised macroscopically, after the loose surrounding tissue has been cleared away, as a yellowish white, lobulated envelope, which renders obscure the course of the bile duct, and which cannot be removed without damage to the duct and gut. It lies not symmetrically round the duct, but mostly on the left side, thus diminishing on the side of the gall bladder. Near the opening of the bile duct into the gut, however, the glandular mass forms a ring round the duct about equally developed on all sides. It consists of a number of lobules, each of which is stated to have a cavity in communication with the lumen of the bile duct. The secretion, then, whatever its nature, would be discharged into the bile duct.

The following notes must be regarded, not as a complete description of the "pancreas" of *Myxine*, but as supplementing the descriptions of MAAS.

Counting the papilla within the lumen of the gut, the bile duct, from gall bladder

* It seems quite possible that the structure described by MAAS had already been discovered by SCHNEIDER in 1879. He says (49, pp. 95–6): "Um die Mündung [of the bile duct in *Myxine*] liegen eine grosse Zahl von Follikeln ähnlich wie bei Ammocötes." There is nothing but the "pancreas" in this neighbourhood to explain such a passage. MAAS quotes SCHNEIDER'S work, but appears to have overlooked his statements relating to *Myxine*.

to gut, had a total length in a 31-cm. Hag of less than 4 mm. Of this the pancreas extended over rather less than the half nearer the gut.

The pancreatic alveoli, the structure of which varies very considerably, are situated within the thickness of the connective-tissue coat of the bile duct, and in fact largely within the serous wall of the gut. They may be found also even at the apex of the papilla on which the bile duct discharges. Usually, however, there are more connective-tissue fibres externally than internally to the alveoli, although I have always found a well-marked zone of connective-tissue fibres between the pancreas and the epithelium of the bile duct.

The pancreas consists of a number of lobules or alveoli clustered round the distal half of the bile duct. There is a vascular plexus round the bile duct, which also passes freely between the lobules of the pancreas, the vessels, however, always remaining outside the periphery of the lobules and never penetrating within them. The whole gland is surrounded by a strong sheath of connective tissue, which further extends freely among the alveoli, separating them from each other. There is no basement membrane to the alveoli, but each is separated from the connective-tissue framework by a very sparse layer of unstriped muscle. The lobules vary greatly in size, a fairly large example having a diameter of 255 μ. Most, but not all, of them have a cavity, generally a relatively large cavity, which may have a diameter of even 195 μ. One specially large alveolus had a diameter of 345 μ and a cavity of 240 μ.

The development of the lobular cavities varies considerably.* In those cases where they are very large and frequent, I still do not find any connection between them and the lumen of the bile duct. Sometimes the cavities of adjacent lobules approximate and are only separated by a narrow partition. Nevertheless I have observed no fusion. Again, spaces may appear sporadically in places outside the region of the pancreas, as, for example, at the gall-bladder end of the bile duct, within the lining epithelium of the duct itself. Instead of one large cavity a lobule may have five or more smaller ones, which appear and disappear in an apparently capricious manner without discharging anywhere. In nearly all cases the cavities are either partly or wholly surrounded by a single layer of epithelium showing numerous mitoses, as in the epithelium of the bile duct, and having in general a close resemblance to the latter epithelium. It is, in fact, difficult to escape the conclusion that the pancreatic lobules are outgrowths from the bile duct.

Very rarely the connective tissue separating an alveolus from the lining of the bile duct is interrupted, and the glandular mass fuses with the biliary epithelium, but only in a few isolated cases have I observed any connection, or any appearance which might be interpreted as a connection, between the cavity of the gland and the lumen of the bile duct. I have even seen the *secretory* section of a gland fuse with the epithelium of

* Since the following paragraph was written I have examined another series of sections, in which all the pancreatic follicles were *homogeneous and solid*, and in which there could be no question whatever of any ducts connecting them with the bile duct. Fusions between certain of the follicles and the epithelium of the bile duct were observed, but these fusions were without the slightest trace of a cavity.

the bile duct—without any connection of the two cavities—whilst the duct portion of the same gland was at the opposite end and turned away from the bile duct. In fact, I find it to be the rule rather than the exception for the duct portions of the lobules to be directed away from the cavity into which they are supposed to open. Indeed, in practically all my preparations the pancreas is a ductless gland, although in saying this I do not wish to claim that such a condition is any other than a secondary and acquired one. The lobules with the largest cavities are often those which are absolutely and indubitably shut off from any connection with the bile duct. Owing to the strong selective staining of the connective-tissue framework, there can be no question here of any error of observation. Further, I have never found that injections thrown into the lumen of the bile duct pass into the cavities of the pancreatic follicles. If the latter were in connection with the lumen of the bile duct, such connections could easily be observed where the connective-tissue sheath is penetrated. In the very few cases where the connection was found, it was easily traced even with the low power of the microscope.

Several pancreatic lobules may fuse and have a perfectly defined epithelial duct with a diameter of 144 μ, and formed by a single layer of epithelium 36 μ high, enclosing a cavity 72 μ across. Such a duct may lose and acquire its lumen in a very curious manner, and finally terminate in a *cul-de-sac* quite apart from the lumen of the bile duct.

Usually the lobules are not isolated, but dichotomise so as to form connected groups after the manner of an acinous gland. Some, however, may be quite independent. There is, in fact, an absence of structural stability one does not usually find in an organ of functional importance. The pancreas occurs only on one side of the bile duct, until shortly before the latter opens into the gut, when it completely surrounds the bile duct like a ring. The alveoli contain sometimes a colourless liquid, and sometimes a granular substance including variously-sized particles—some of them quite large, and others having a concentric appearance—staining an intense black with iron hæmatoxylin. Here and there one finds a single disintegrating cell in the alveolus.

The glandular as distinct from the epithelial portion of the lobule has a somewhat complex structure. The nuclei are oval or round and have precisely the same appearance as those of the duct portion of the lobule and of the bile duct itself, except that the latter are larger and the chromatic network is somewhat looser and therefore stains more lightly. In some cases a well-defined nucleolus can be seen lying in a clear area. Very few mitoses were, however, observed. The cell outlines are sometimes difficult, or even impossible, to define. In other cases they appear quite clearly, and the gland cells are then seen to be irregular in shape and to vary in size. The cytoplasm is a loose, faintly staining reticulum, and not granular. It may contain large non-staining spaces. Inter- or intra-cellular cavities as described by MAAS I have not observed; but these, like bile capillaries, may depend on the state of activity of the gland. A tangential section of a lobule shows what might be interpreted as inter-cellular cavities, but these on examination turn out to be the inter-lobular blood capillaries. I am speaking now of

material specially fixed by *intra-vitam* injection, in which I do not find any specially modified cells associated with the possible existence of inter- or intra-cellular spaces. Further, the gland cells of the pancreas have certainly not the appearance of an enzyme-secreting gland, but if anything that of a mucin gland.

The fundamental point of difference between MAAS' results and my own is that he describes the secretion of the gland, whatever it may be, as discharged freely into the bile duct, whilst in my material the gland is to all intents and purposes a ductless one. I have no doubt we have both correctly described the material at our disposal as we found it, and that the difference in our results is only one more indication of the existence of distinct races or varieties of *Myxine glutinosa*. It is clear that the pancreatic lobules represent outgrowths of the bile duct, and are hence, at least originally, in free communication with it. It seems therefore that the absence of the efferent channels in my material indicates a retrogressive change, and that the gland is either losing the importance it formerly possessed, or undergoing some functional modification.

Owing to the small size of the gland, and the great difficulty of satisfactorily isolating its secretion, I do not think it possible to test the latter by biochemical methods. It would mean dissecting it out in at least 100 specimens; and even if this could be done in the necessary time, one could never be certain that the extract was free from the secretion of the liver.

H. THE THYROID GLAND (Figs. 3 and 12).

In a preliminary paper (13) I briefly described the structure of the thyroid of *Myxine*, under the impression that it had up to that time escaped notice. SCHAFFER, however, pointed out that the Myxinoid thyroid had been described by W. MÜLLER in an obscure paper in 1871, and at the same time he added an account of this structure in *Myxine*. I shall, therefore, now confine myself to such details as are omitted in SCHAFFER'S description.

As shown in fig. 12, which represents a transverse section through the region of the gills, there is a column of loose fatty tissue in the middle line, wedged in between the gills, and extending from the gut above to the cardiac aorta below. In this column of fatty tissue are embedded the small vesicles which represent an unpaired, diffuse, scattered thyroid, and which can be seen with the naked eye (*thy.*).

The thyroid at first sight does not appear to be an important organ in the adult. In fig. 12, which in this particular series showed the maximum number of thyroid vesicles appearing in any one section, only eight are seen, and the gland certainly does not strike one from the point of view of size. Fortunately, however, I plotted it out from my large series of sections, and the result is given in fig. 3. Nothing could be more striking. The gland extends over a considerable area, both vertically and longitudinally, and it includes in this individual 251 vesicles of all sizes and shapes. If these were massed together into one compact gland, we should have, compared with the size of the animal, a large and obviously important structure.

All the vesicles are closed and have no connection with each other, and, as I pointed out in my preliminary paper, the thyroid of *Myxine* in this respect resembles that of Teleosts. SCHAFFER has found, exceptionally, some of the alveoli dorsal to the œsophagus, which is contrary to my experience. In my large series of sections the vesicles commence somewhat in advance of the first pair of gills at section 2096 (cp. the chart, fig. 3). These anterior vesicles are flattened dorso-ventrally, and are therefore wide from side to side, and although the wall consists of the usual thyroid epithelium, only a very slight cavity and contents were observable in the sections. In fact, the anterior vesicles are difficult to find, and can hardly be important functionally. They are closely attached to the thick tough membrane which here binds together the copulo-copularis and perpendicular muscles and the two chondroidal bars, and they are situated immediately over the superior chondroidal bar. The most posterior vesicles do not extend much behind the origin of the last afferent branchial artery, and not so far back as the posterior border of the last gill. At this point the gut becomes deeper dorso-ventrally, and descends to enter the anterior cœlom.

The form and size of the vesicles vary enormously, although most of them are small and circular or oval. In the specimen figured the large and irregular vesicles were confined to the ventral region of the thyroid area, but this may not apply to all cases. SCHAFFER does not appear to have realised the true form of the alveoli, having evidently only studied detached sections without reconstructing entire alveoli.

Admirable preparations illustrating the histology of the thyroid may be obtained by *intra-vitam* injection of the fixative from the heart. I have used mostly Mann's picro-corrosive-formalin. This travels through the vessels with great rapidity—much faster than any coloured injection medium, and the whole animal is fixed throughout in a fraction of a minute, as can be demonstrated by opening up the body in various places immediately afterwards. I find the best stain for *Myxine* tissues generally is iron alum hæmatoxylin, followed by eosin.

The wall of the thyroid vesicles consists of a single layer of epithelium, in average cases about 20 μ high. This may be quite flat and simple in structure, or the cells may be fairly tall and with well-marked intra-cellular contents. Generally they exhibit a well-marked resemblance to the thyroid vesicles of other vertebrates. There is, as in man, no basement membrane *sensu stricto*. It is true the vesicles are enclosed in a sheath, but this is formed by, and belongs to, the surrounding connective tissues. That it is no part of the vesicle is well seen where two vesicles are in close contact. The supposed basement membrane passes across from one vesicle to the other, leaving the contiguous surfaces bare. Or in those cases where a vesicle is closely opposed to the ventral wall of the gut, it will be noticed that the abutting surface of the vesicle is without a membrane.

The histology of the thyroid cell varies very greatly according to its condition of activity. The nuclei are well marked and vesicular. There is a distinct nuclear membrane, and a reticulum with a somewhat dotted chromatic material and nucleoli. Apart

from the nucleus, the contents of the cell vary considerably, not only in appearance but in staining reactions. Sometimes we can distinguish intra-cellular bodies of two kinds, which may, however, both occur in the same cell. First, there are large waxy bodies, which vary in consistency, and lie in a clear area or vacuole. In their early (?) stages these stain faintly with eosin and iron hæmatoxylin. Then there are the smaller spherical bodies, which may be very numerous and variable in size, and appear to resemble the zymogen granules of other secreting cells. They stain intensely with iron hæmatoxylin and eosin. The former have been described by SCHAFFER, but they are not invariably present, whilst the latter he does not mention. In some cases where these two intra-cellular products are extremely developed, the nuclei are indistinct, and only stain faintly. There are many indications that the larger intra-cellular bodies are formed by the fusion of the smaller ones.

When there is a single large intra-cellular product present it lies, as a rule, either on the peripheral or the central side of the nucleus. SCHAFFER states that it occurs only rarely at the peripheral end of the cell, but this statement appears to be based on the examination of an insufficient number of individuals, since it may be found more often peripherally than centrally, and in some cases I have found it almost exclusively on the outer side. In a few cases there are two products in one cell, which may be either together central or external to the nucleus, or separated, with the nucleus crushed between them. These products in isolated cases may be extruded bodily from the cell into the cavity of the vesicle.

SCHAFFER figures one condition which I have not seen, although I do not on that account question the accuracy of his observation. Here the nucleus is pushed to the periphery of the cell, and is greatly compressed from side to side so as to assume a rod-like form, whilst the central portion of the cell is occupied by a large, oval, feebly staining secretion product, surrounded by a sheath or "theca."

The contents of the vesicles are again very variable. Usually they appear quite empty in the sections. Occasionally one finds a coagulated substance of a granular appearance, and only very rarely, as SCHAFFER also finds, is there present the colloidal substance so characteristic of the thyroid vesicles of higher vertebrates.

The thyroid of *Myxine* was first described by W. MÜLLER in 1871 (43) in the following words: "Dagegen ist mir der Nachweis des Organs in der Classe der Cyklostomen bei *Myxine glutinosa* gelungen, welcher die Schilddrüse bisher allgemein abgesprochen worden ist. Sie liegt hier in der fettreichen Bindegewebslamelle, welche sich von der Ventralfläche des Œsophagus zur oberen Fläche des Kiemenarterienstammes in dessen ganzer Ausdehnung erstreckt und besteht aus einer ziemlich beträchtlichen Zahl theils zerstreut liegender isolirter, theils zu kleinen Gruppen von 2–5 vereinigter rings geschlossener Follikel. Letztere sind theils von kugeliger, theils von ellipsoidischer Gestalt, der Durchmesser der ersteren schwankt zwischen 0,1 und 0,25 der Längendurchmesser der letzteren erhebt sich bis zu 0,4. Sie bestehen aus einer dünnen Membrana propria und dieser aufsitzendem einschichtigem Epithel. Die Zellen des letzteren

sind theils cubisch, 0,008 im Durchmesser, theils cylindrisch, 0,012 hoch, 0,008 breit, sämmtlich mit Kernen von durchschnittlich 0,006 und 1–2 Kernkörperchen und sehr zartem, feinkörnigem Protoplasmakörper versehen. Das Epithel umschliesst eine scharf begrenzte mit klarer, farbloser Flüssigkeit gefüllte Höhle." This description, though brief, admits of no doubt as to MÜLLER having seen the thyroid of *Myxine*. The same writer a year later * describes the thyroid of the adult lamprey as extending below the longitudinal "tongue" muscle from the second to the fourth pair of gill sacs.

The development of the Myxinoid thyroid has been studied by STOCKARD in *Bdellostoma* (53). He finds that it arises as a median, unpaired "downpushing from the ventral floor of the pharynx throughout the entire gill area." This forms a long trough with a restricted lumen, which subsequently becomes separated from the gut, and breaks up to form the isolated vesicles of the adult. "The chief point of interest shown by the trough-like thyroid anlage is the very extensive gut area from which it is derived; in no other vertebrate does the thyroid evagination from the pharynx run through so relatively long an area" (p. 95). "It will now be clearly seen that although the adult condition of the thyroid in Myxinoids and Teleosts are readily comparable, the developmental processes through which the ends are reached seem widely different" (pp. 97–8). Judging from the recent work of FERGUSON and GUDERNATSCH, the thyroid is a remarkably uniform structure throughout the Chordate series.

J. CLOACA (Fig. 5).

The cloacal aperture is an elongated longitudinal slit compressed from side to side, 9 mm. long in a 36-cm. Hag, and $4\frac{1}{2}$ cm. from the extremity of the tail. The anatomy of the cloacal region was first fully described by R. H. BURNE (12). If an incision be made from the anterior extremity of the cloacal aperture and continued a short distance along the rectum, and the walls pinned out, it will be noted that the anus (*an.*) opens into the cloaca (*cl.*) anteriorly and ventrally by a larger puckered aperture. The roof of the rectum (*an.'*) is continued backwards across the cloaca at the sides, but not at the middle line, and thus the cloaca is divided imperfectly into a dorsal and a ventral chamber. Both chambers bear folds. In the one case they are continued backwards from the margin of the genital pore, and in the other they are the direct continuations of the rectal folds. The ventral chamber receives the anus, as already mentioned. Into the dorsal chamber there opens in front, and of course dorsal to the anus, the single, conspicuous, round abdominal pore, or porus genitalis (*p.g.*), surrounded by a thick fibrous band (*p.g.'*). This pore was first described by A. M. C. DUMÉRIL in 1807, in *Myxine*, and afterwards by J. MÜLLER. From the porus genitalis there passes backwards right to the posterior end of the cloaca a narrow but obvious median dorsal ridge. Somewhat in front of the middle of this ridge there is a thickening, the urinary papilla (*ur.pp.*), and an examination of this thickening with a lens reveals two small

* *Jena. Zeits.*, Bd. vii., 1872.

asymmetrical openings—the apertures of the segmental ducts (*s.d.*) The left seems to be the larger, and is certainly anterior to the right. There thus appears to be in *Myxine*, in this dorsal cloacal chamber, a representative of the distinct and undoubted urogenital sinus of the lamprey, but BURNE argues with much reason "that the urogenital sinus of the lampreys is absent in the Myxinoids, and that in the latter the anus, 'porus genitalis,' and ureters open into an integumentary cloacal chamber, similar to the cloacal chamber common to anus and uro-genital sinus in the lamprey" (12, pp. 494–5).

According to BURNE, the porus genitalis is surrounded by a large diffuse gland, the histology of which is said to make it highly probable, in spite of its deep position, that it represents modified lateral slime glands. As will be seen on reference to fig. 5, the slime glands (*s.s.*) are apparently absent from the two myotomes (89, 90) of the cloacal region, and when it is remembered that the supposed genital pore gland completes the only break in this linear series, and that the true slime glands immediately posterior to it are also largely covered by the caudal muscles (cp. Part II., fig. 4), this conclusion receives some support. The gland is stated to have several openings in the neighbourhood of the margin of the pore. Its function may be, as BURNE suggests, either to lubricate the pore during oviposition, or to occlude it by a waxy secretion, and thus prevent access of foreign matter to the abdominal cavity. These suggestions, however, disregard differences which should exist in relation to sex, and also the fact that the genital pore is closed by the action of the sphincter cloacæ. I shall discuss the alleged anal slime gland in a subsequent passage.

The hind-gut has only a short course. It is easily distinguished from the mid-gut by its sharp, acute, and somewhat irregular folds, which have no lymphoid packing, and are similar to those of the fore-gut in having an epithelial investment of several layers of cells. The lining of the cloaca even more resembles the epithelium of the outer skin.

I have already drawn attention (cp. Part I., p. 786) to the thin sheet of cartilage described by AYERS and JACKSON in the wall of the cloaca of *Bdellostoma*. I have described in the section on the gut the only representative of cartilaginous tissue which occurs in the cloacal region of *Myxine*.

An original figure of the cloacal region and tail of *Myxine glutinosa* is given by GOODRICH in his masterly treatise on Fishes in LANKESTER'S *Zoology* (p. 33).

Since the above was written I have made and examined serial sections of the cloaca of a 19-cm. and a 25-cm. Hag. In both cases the segmental duct expanded posteriorly into a kind of sinus. From this expansion, which ends blindly behind, there is given off internally another and terminal duct,* which at once bends mesially, dips *under* the sphincter cloacæ, and, passing downwards and backwards, opens at the urinary papilla as above described. Now the place where this terminal duct is given off coincides precisely with the boundary between the mid- and hind-guts, and it is therefore highly interesting to note: (1) that the lining of the segmental duct consists

* A somewhat similar condition is figured by BURNE in *Bdellostoma*.

of a single layer of cells, but that of the terminal duct of many layers of cells; (2) that the two epithelia bevel into each other exactly as they do at the mid- and hind-gut boundary (cp. description of gut); and (3) that the glassy and granular mucous cells characteristic of the epidermis *may* occur at *any* part of the terminal duct. In the 19-cm. Hag the two terminal ducts open separately and symmetrically, but in the 25-cm. specimen the openings were asymmetrical, as already described in the mature animal. It seems natural to conclude that the segmental duct terminates at the anterior border of the constrictor cloacæ in the sinus-like swelling, and that the terminal duct is simply an integumentary (epidermal) pocket. It must, however, not be forgotten that on similar grounds we should have to regard the whole of the pharyngeal gut as epidermal, and this we know to be contrary to fact.

In one respect the description given above is directly contrary to the following statement by BURNE. He says: "Now in the adult myxinoid the ureters do not imperceptibly pass into the cloacal chamber, as they do into the urogenital sinus of the lamprey, but open upon a raised papilla; *upon the margin of the ureteric opening, the epithelium changes its character—inside, it is similar to that lining the rest of the ureter; outside, it is epidermic*" [italics mine].

In the transverse sections of the 19-cm. Hag the rectum fuses ventrally with the abdominal wall at the anterior ventral margin of the sphincter cloacæ, and further back the whole fuses with the skin at the boundary between mid- and hind-guts. The gut is now connected with the roof of the abdominal cavity by the deep median dorsal mesentery. Then the striated sphincter cloacæ rises round and over the roof of the gut and splits the body cavity into two portions, placed one over the other, and each divided by a median vertical partition — the posterior continuation of the mesentery. The dorsal pair of cavities soon die away, the left one first. The ventral pair one naturally expected to open posteriorly at the genital pore. The median mesenteric partition, first of all, becomes imperfect ventrally, but the dorsal portion remains suspended from the roof of the cavity almost to its posterior extremity. The cavity becomes narrowed and surrounded by a dense cellular connective tissue, which finally fuses with the upper section of the cloaca, but the lumen *ends blindly without opening anywhere.* There was, therefore, no porus genitalis in this specimen, *nor the slightest trace of the anal slime sac* described by BURNE. In the series of longitudinal sections of the 25-cm. Hag the constrictor cloacæ does not partition the body cavity as above described, but passes entirely above it. The posterior blind extremity of the body cavity bends downwards and backwards, and approaches a blind epidermal cloacal pocket. The two are separated by a plug of cellular connective tissue. A close examination of this plug reveals phagocytic operations in its central core, and there is no doubt that in this specimen the genital pore was in the act of breaking through. This, of course, may happen at different sizes according to sex and conditions of maturity. In this example also there were no signs of the anal slime sac. Hence the genital or abdominal pore of *Myxine* is to be found only in the mature animal. It

should be noted that the constrictor cloacæ, by enclosing the anus, genital pore, and segmental ducts, will occlude all three at the same time.

To add a still further note to the above, I have now, by the courtesy of Mr R. H. BURNE, examined his sections of the cloaca of *Myxine*. I find in the ureter that the change from the single- to the many-layered epithelium occurs precisely as in my own sections. The statement by Mr BURNE, quoted above, that the epithelium changes at the margin of the ureteric opening, is therefore incorrect. The only difference of importance is that in Mr BURNE's sections I find no glassy or granular mucous cells in the terminal duct. These are, however, not numerous in my sections, and they may, of course, disappear in the adult. With regard to the anal slime sac, Mr BURNE has been somewhat, and naturally, misled by not having examined sections of younger material. The structure in question is undoubtedly what I have called above the dorsal chamber of the cloaca, into which the genital pore opens, and the "semicircle of openings" of the anal slime sac are simply the spaces between the folds into which the lining of the cloaca generally is thrown. The dorsal chamber is naturally present in my sections; but, although it is crowded with the glassy and granular mucous cells, it never occurred to me to identify it with Mr BURNE's anal slime sac, since these cells occur just as numerously in another region of the cloaca. I can, however, confirm Mr BURNE in one important respect, *i.e.* in the presence of the peculiar thread cells in the dorsal chamber of the cloaca which are found elsewhere only in the lateral slime sacs of the skin. Also the epithelium is crowded with the glassy mucous cells, but there are no granular cells. In my preparations there are numerous granular cells, but no thread cells. The slime sac character of the dorsal chamber of the cloaca therefore develops late, and there is little doubt that the thread cells are produced by modification of the granular cells. There is no occasion to conclude that the dorsal chamber is a modified slime gland or glands. The whole skin produces glassy mucous cells and thread cells of a type, as shown by G. RETZIUS, and the fact that the slime sac characters have not been fully assumed in a 25-cm. Hag would indicate that the conversion of the dorsal chamber of the cloaca into a kind of slime sac is a new and independent feature.

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L. EXPLANATION OF PLATES.

REFERENCE LETTERS.

a.d.p. Anterior arch of the dental plate.
a.h.d. Anterior hepatic duct.
a.h.v. Anterior hepatic vein.
a.l.l. Anterior lobe of the liver.
an. Anus.
an.' Posterior extremity of roof of anus partially dividing cloaca into two chambers.
a.p.v. Anterior portal vein.
a.s. "Aquæductus Sylvii," or forward prolongation of the mesencephalic ventricle.
b.d. Bile duct.
b.g. Biliary gland or "pancreas."
b.o. Bulbus olfactorius.
b.p. Pad of soft pseudo-cartilage at the anterior end of the anterior segment of the basal plate.
b.p.$^{1-3}$ Anterior, middle, and posterior segments of the basal plate.
br.a.^{1} "First branchial arch."
br.a.^{2} "Second branchial arch."
br.ap.' Left, *br.ap.''* Right } external branchial apertures.
br.cl. Branchial cloaca.
c.ao. Ventral or cardiac aorta.
c.b.c.' Paired anterior limb of the M. constrictor branchiarum et cardiæ.
c.b.c.''' Second loop of the same muscle.
c.b.c.'''' Third loop of the same muscle at the bend (cp. Part II., fig. 2).
c.c. Cornual cartilage.
c.e. External head, *c.e.'* Internal head, *c.e.''* Fused external and internal heads } of the M. copulo-ethmoidalis.
c.g.p. Tendon of the M. copulo-glossus profundus, the protractor muscle of the dental plate.
c.g.p.' Lateral head, *c.g.p.''* Median head } of the M. copulo-glossus profundus.
c.g.s. M. copulo-glossus superficialis.
c.g.s.' Median slip of tendon of above to ventral skin.
c.g.s.'' Lateral slip of same tendon.
c.h. M. cranio-hyoideus.
cl. Cloaca.
cœ.a. Cœliac artery.
c.p.', *c.p.''*, *c.p.'''* } M. constrictor pharyngis—first, second, and third divisions.
cp.c. M. copulo-copularis.
c.pl. M. copulo-palatinus.
cp.t.c. Principal head, *cp.t.c.'* Posterior division, *cp.t.c.''* Anterior division } of the M. copulo-tentaculo-coronarius.
c.p.v. Common portal vein.
c.q.p. M. copulo-quadratus profundus.
c.q.s. M. copulo-quadratus superficialis.
d.m. Area of mucosa immediately behind the dental apparatus puckered by the withdrawal of the latter. It flattens out when the teeth are protruded.

d.æs.ct. Ductus œsophago-cutaneus.
d.t. Median dorsal tooth.
d.t.' Curved median bar of soft pseudo-cartilage, containing nodules of true (soft) cartilage, arising from the base of the median dorsal tooth, and curving backwards round the anterior margin of the palatine commissure to be attached to the posterior extremity of the subnasal bar.
e.b.p.' External bar of the anterior segment of the basal plate.
e.l.b. External lateral velar bar.
e.l.b.' Short rod of soft cartilage connecting *e.l.b.* with the posterior extremity of the inferior process of the "pterygo-quadrate."
f.$^{1-4}$ The four fenestræ of the skull.
f.r. The so-called "fin rays" composed of soft cartilage.
g.b. Gall bladder.
g.l. Gill lamella.
h.c.g. M. hyo-copulo-glossus.
h.c.g.' Anterior end of "tendon" of *h.c.g.*
h.c.g.'' "Tether" of *h.c.g.*
h.c.p. M. hyo-copulo palatinus.
h.g. Habenular ganglion of the diencephalon. The shaded portion is the pineal organ.
h.p. Hypophysial plate.
h.p.' Rod connecting *h.p.* with the posterior transverse bar of the nasal capsule.
h.p.'' Hypophysial plate + the fused rod *h.p.'*
hy. "Hyoid" arch.
hyp. Hypophysis cerebri.
i.b.p.' Internal bar of the anterior segment of the basal plate.
i.c.b. Inferior chondroidal bar.
i.l.b. Internal lateral velar bar.
i.l.c. Inferior lateral cartilage.
inf. Infundibulum cerebri.
int. Intestine or mid-gut.
l.l.c. Lateral "labial" cartilage.
l.lg. M. longitudinalis linguæ.
l.lg.^{a} Peripheral tendon } of *l.lg.*
l.lg.^{b} Central tendon. }
l.p. Lateral plate of the nasal capsule.
l.p.c. Large left posterior cardinal vein.
mc. Mesocœle, or mesencephalic ventricle.
m.e. Mesencephalon.
mes. Median dorsal mesentery.
mes.' Ventral fusion of rectum with body wall forming a rudimentary median ventral mesentery.
mes.'' Oblique dorso-posterior extension of above fusion.
mt.e. Metencephalon.
mth. Mouth.
n.a. External opening of the nasal tube.
na.ph. Naso-pharyngeal or hypophysial tube.
nas. M. nasalis.
n.c. Nasal capsule.
*n.r.*8. Eighth ring of the nasal tube (cp. Part III., fig. 1).
nt. Chorda dorsalis.
n.tb. Nasal tube.
o.a. Oral aperture.
obl. M. obliquus.
oes. "Œsophagus," or properly the pharyngeal gut.
o.l. Olfactory lamina.
par. M. parietalis, forming the myotomes.
pc. "Parachordal" cartilage.
p.d.p. Posterior arch of the dental plate.
p.e. Prosencephalon.
p.e.p. M. palato-ethmoidalis profundus.
p.e.s. M. palato-ethmoidalis superficialis.
p.g. Porus genitalis (abdominal pore).
p.g.' Thickened fibrous band surrounding the porus genitalis.
p.h. Portal heart.
p.h.d. Posterior hepatic duct.
p.h.v. Posterior hepatic vein.
pl. "Palatine" bar.
pl.c. External head } of the M. palato-cor-
pl.c.' Internal head } onarius.
pl.cm. "Palatine" commissure.
p.l.l. Posterior lobe of the liver.
pn. Pronephros.
pp. M. perpendicularis.
p.q. "Pterygo-quadrate."
p.t.v.b. Posterior transverse velar bar.
p.v. Portal or supra-intestinal vein.
q.p. M. quadrato-palatinus.
q.p.' Tendon of *q.p.*
rect. M. rectus.
r.intest.X. R. intestinalis vagi.
r.p.c. Smaller right posterior cardinal vein.
s.ao. Dorsal or systemic aorta.
s.d. Segmental duct.
s.i.v. Sub-intestinal vein.
s.l.c. Superior lateral cartilage.
sn.b. Subnasal bar.
sp. Spermatic portion of the hermaphrodite gonad.
sp.cd. Spinal cord.
sp.sk. Suprapharyngeal skeleton.

sp.sk.' Anterior, *sp.sk''* Median. } connecting processes of *sp.sk.*
s.s. Slime sacs—numbered from before backwards.
sy. "Sympathetic" nerve, formed by the fusion of the two RR. intestinales vagi.
thy. Thyroid vesicle.
t.o. M. transversus oris.
t.p. M. tentacularis posterior.
tr. "Trabecula."
ur.pp. Urinary papilla and apertures.
vel. Pharyngeal velum.
v.q. Ventral division, *v.q.'* Middle division, *v.q.''* Dorsal division } of the M. velo-quadratus.
v.qt. Ventriculus quartus.
v.s. M. velo-spinalis.

Plate I.

Fig. 1. Median vertical longitudinal section of a 26½-cm. Hag. × 8⅓. The drawing is necessarily based on the study of a number of sections immediately about the median plane, and was originally sketched out with Edinger's projection apparatus. Care has been taken to make it as accurate as possible. Visceral cavities, shaded; vascular spaces, red; hard and soft cartilage, green; pseudo-cartilage, obliquely striated. The tentacles and nasal rings are numbered from before backwards, and the isolated spaces in the anterior portion of the brain represent vestiges of the ventricular system.

Fig. 2. Reconstruction from serial sections of the branchial apparatus of a 25-cm. Hag, seen from the ventral surface. × 9½. The shape of the third pair of gills is somewhat exaggerated owing to the fact that the specimen had to be cut into three pieces to get it into the microtome, and one of the two breaks was through this region. Gills, afferent and efferent ducts, and the external branchial apertures displayed laterally, in order that all may be shown, but the position of all the structures in the longitudinal plane is, of course, correctly indicated. Outer and inner surfaces of gills not differentiated. Ventral or cardiac aorta, red. Afferent and efferent gill ducts numbered from before backwards.

Plate II.

Fig. 3. Reconstruction of the detached vesicules (251 in number) forming the thyroid gland of a 25-cm. Hag, viewed laterally from the left side. × 11. For the reason mentioned above, the length of vesicle * is somewhat exaggerated, which explains also the gap between sections 2560 and 2600. A few of the alveoli are represented displaced vertically for the sake of clearness, but only occasionally do the vesicles overlap in the transverse plane. Similarly the club-shaped muscle has been slightly depressed, so as not to overlap the anterior vesicles. Afferent gill ducts numbered from before backwards. Cardiac aorta, red; and afferent branchial arteries shown cut off short.

Fig. 4. Dissection from the ventral surface of the portal heart, gall bladder, and adjacent region of a 38-cm. Hag. × 3. The two lobes of the liver, with the gall bladder, have been turned to the left and pinned down. Hepatic ligament and cystic peritoneum (together with the proximal portion of the cystic vein) removed. Intestine displaced slightly to the right. Heart removed. Arteries, cross-striated.

Fig. 5. Dissection from the right side of the cloacal region of a 37-cm. Hag. × 4. Myotomes and slime sacs numbered from before backwards, the former being also partly cut away. Segmental duct dissected clear and displaced dorsally. Sphincter cloacæ, and right wall of cloaca, body cavity, and abdominal pore removed.

Plate III.

Fig. 6. Simplified diagrammatic horizontal section of the Myxinoid gill. × 17. The number of gill lamellæ is greater than that shown. The upper part of the section represents the appearance of a tangential section, the lower part that of a central section. Afferent arteries, blue; efferent arteries, red; water spaces, shaded.

Fig. 7. Section number 240 of the large series of a 25-cm. Hag. × 12½. This set of five sections is intended to illustrate the relations of the anterior region of the gut. All were drawn with Edinger's projection apparatus. As regards the skeleton, the sections should be compared with the charts accompanying Part III. of this work. Muscles indicated by circles; vascular spaces of whatever character, red; cartilage, green; pseudo-cartilage, obliquely striated; cavity of mouth and nasal tube, shaded.

Fig. 8. Section number 390. × 12½. Colours, etc., as above. The section passes through the anterior process of the hypophysial plate, and through the anterior region of the anterior arch of the dental plate. The numbers refer to the *outer* row of the ventral teeth—1, 1′, 2, 3 = the anterior and posterior cusps of tooth 1, and teeth 2 and 3.

Fig. 9. Section number 510. × 14. Colours, etc., as above. The section passes through the thalamus of the brain immediately in front of the infundibulum—in fact, a small portion of the infundibular cavity appears in the section. The third, fourth, and fifth teeth of the inner row of ventral teeth, and the sixth, seventh, and eighth teeth of the outer row, are indicated by numbers. Cavity of naso-pharyngeal (hypophysial) tube, shaded.

Plate IV.

Fig. 10. Section number 720. × 10. Colours, etc., as above. The section passes through the pharynx after the latter has been joined by the naso-pharyngeal tube with its lateral diverticula and also through the base of the velum or pharyngeal valve which projects boldly into the pharyngeal cavity.

Fig. 11. Section number 840. × 9½. Colours, etc., as above. The section passes through the velum or pharyngeal valve just anterior to the anterior transverse velar bar (cp. Part I., fig. 16, and Part III., fig. 2), and illustrates the relation of the valve to the cavity of the œsophagus, and also the relative position of the "branchial" arches.

Fig. 12. Section number 2680. × 10. Colours, etc., as above. Efferent gill ducts numbered from before backwards. An afferent branchial artery is shown entering the third gill on the right side, and an efferent branchial artery leaving the fourth gill on the left side. The section passes through practically the centre of the gill region (cp. fig. 2), and is intended to illustrate the topographical relations of the thyroid vesicles.

Fig. 13. Section number 3550. × 10. Colours, etc., as above. To illustrate the relations of the biliary apparatus generally. The figure is diagrammatic in one respect, since the whole of the bile duct does not appear in one section. Its relations are, however, correctly shown. On the left side a dorsal root of a spinal nerve with its ganglion are shown. On the right the section shaves the efferent duct of the thirty-fifth slime sac (counting from before backwards).

PROF. F. J. COLE ON THE MORPHOLOGY OF MYXINE.—PART V. PLATE I.

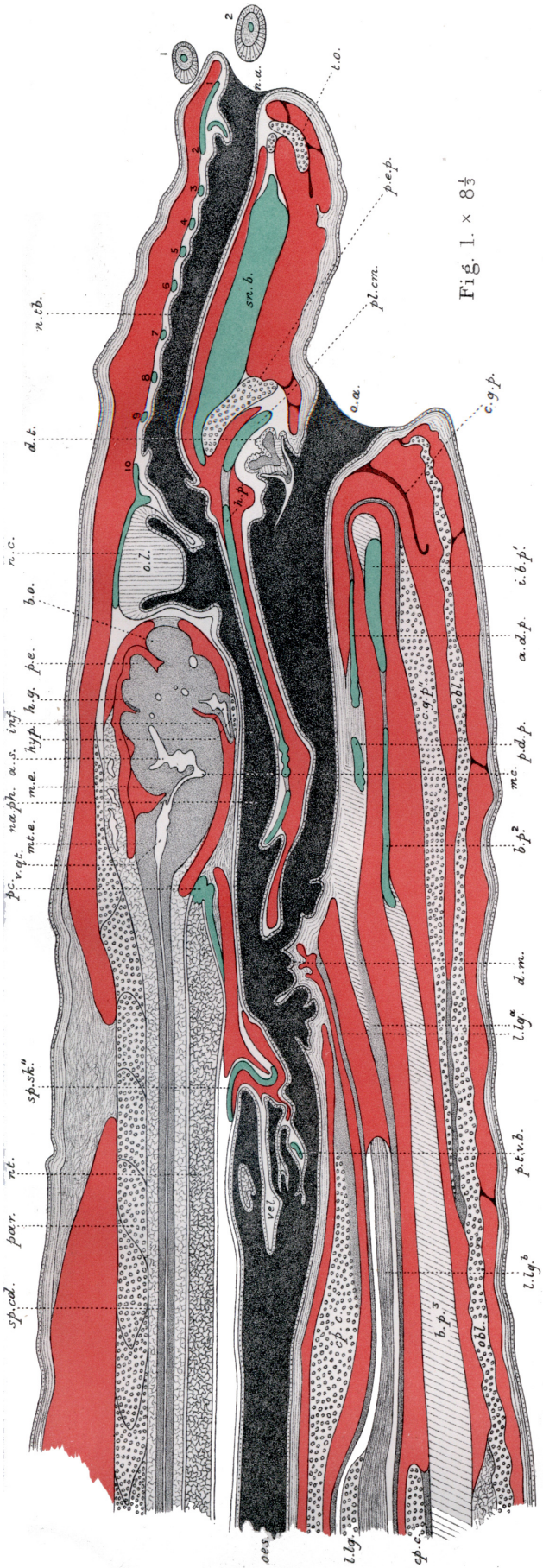

Fig. 1. × 8½

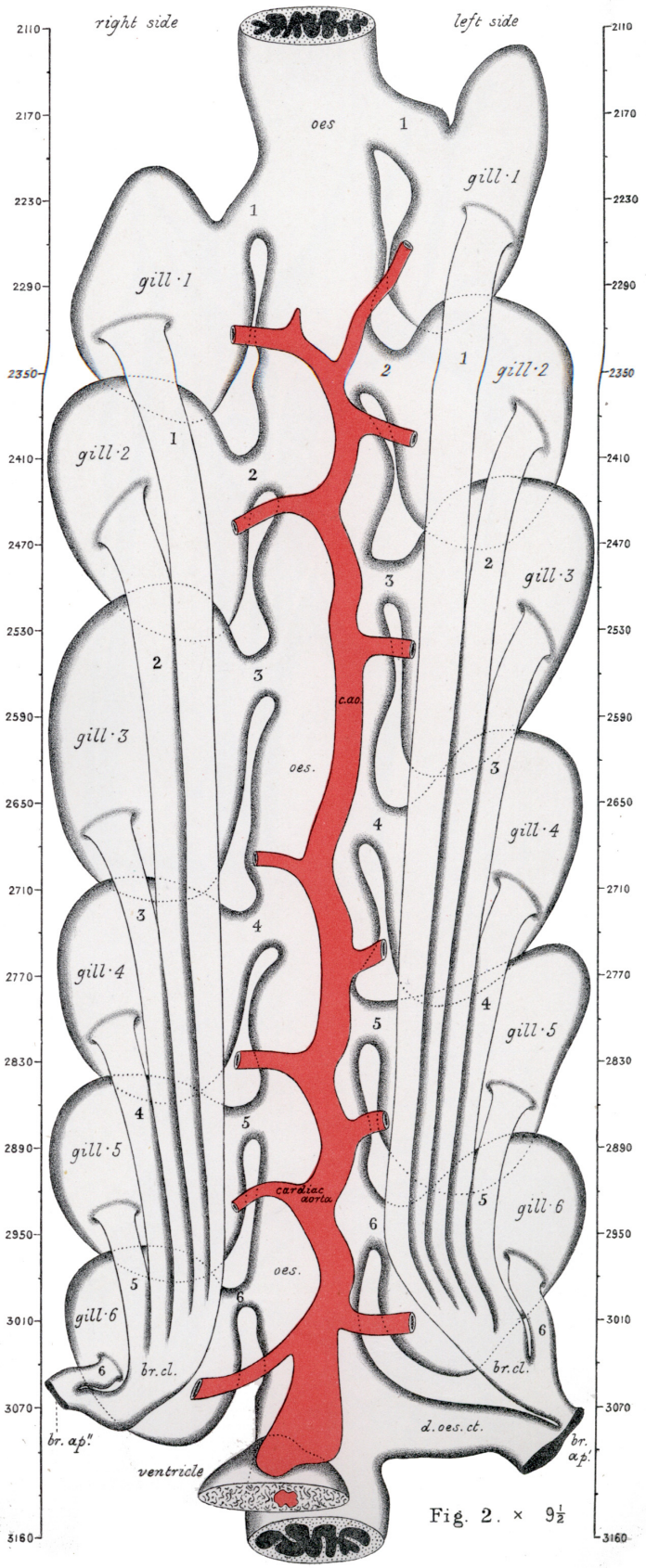

Fig. 2. × 9½

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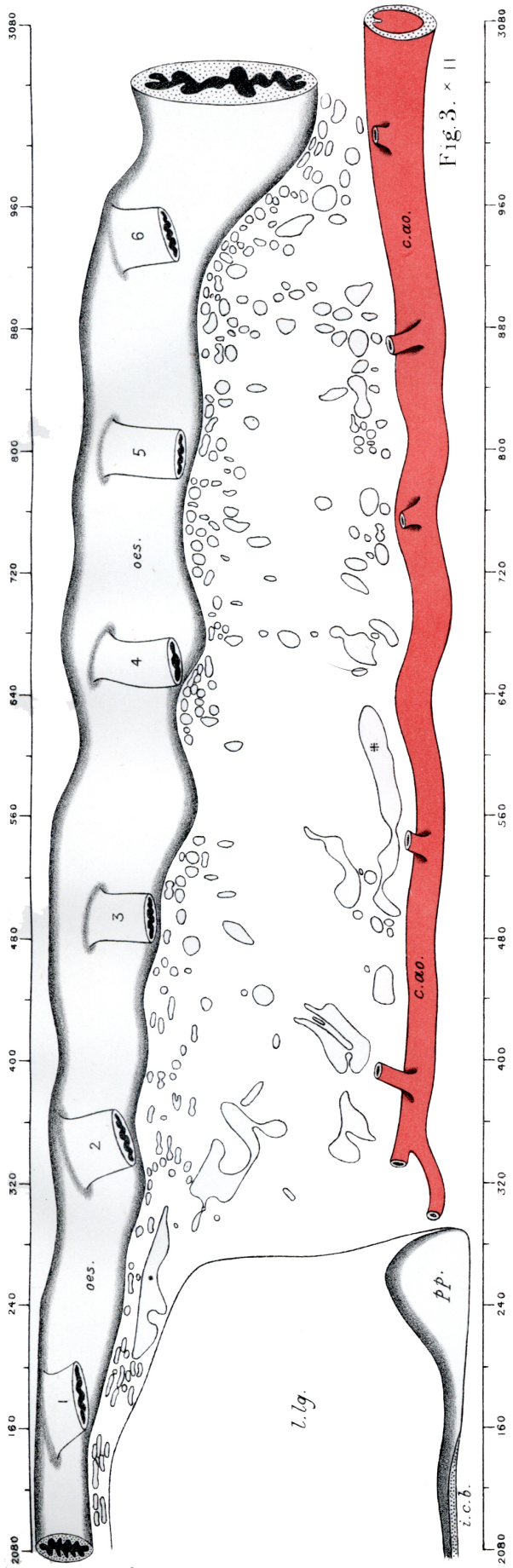

Fig. 3. × 11

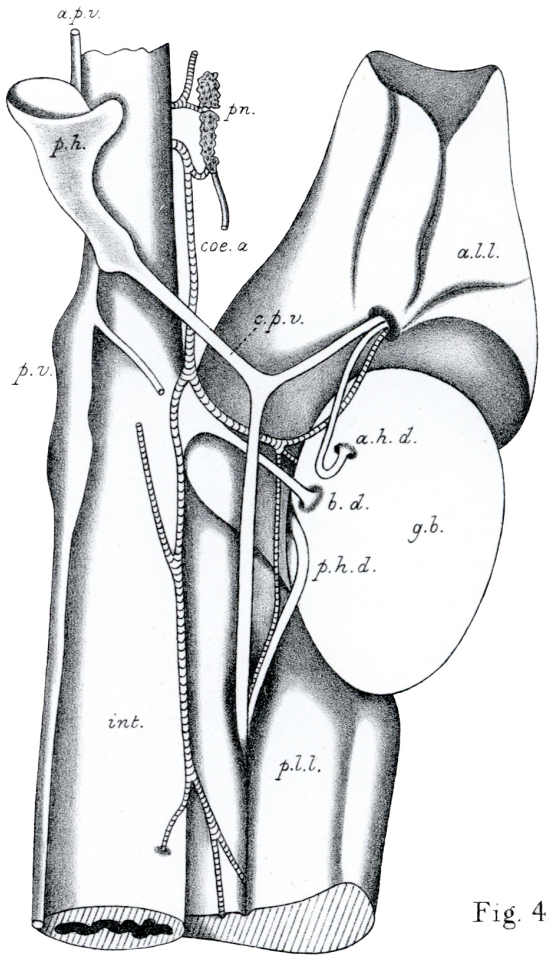

Fig. 4. × 3

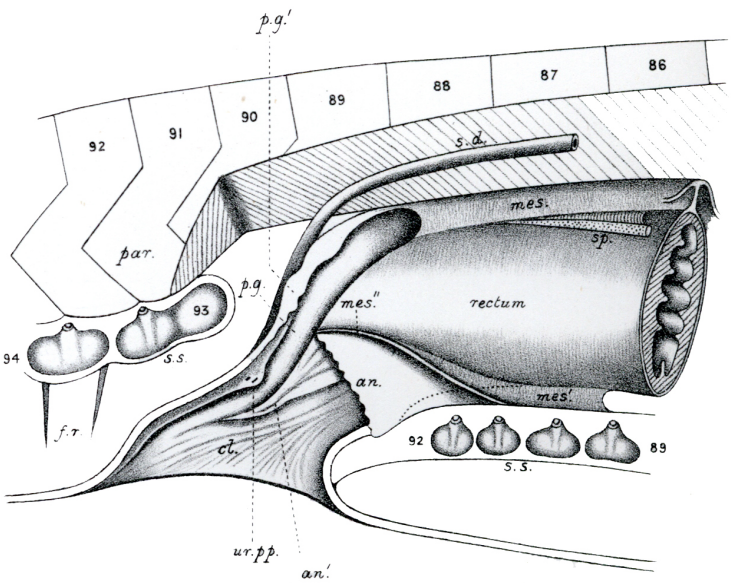

Fig. 5. × 4

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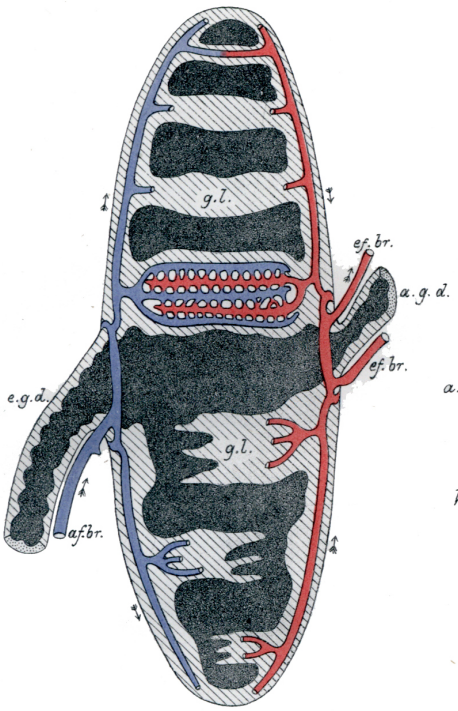

Fig. 6. × 17

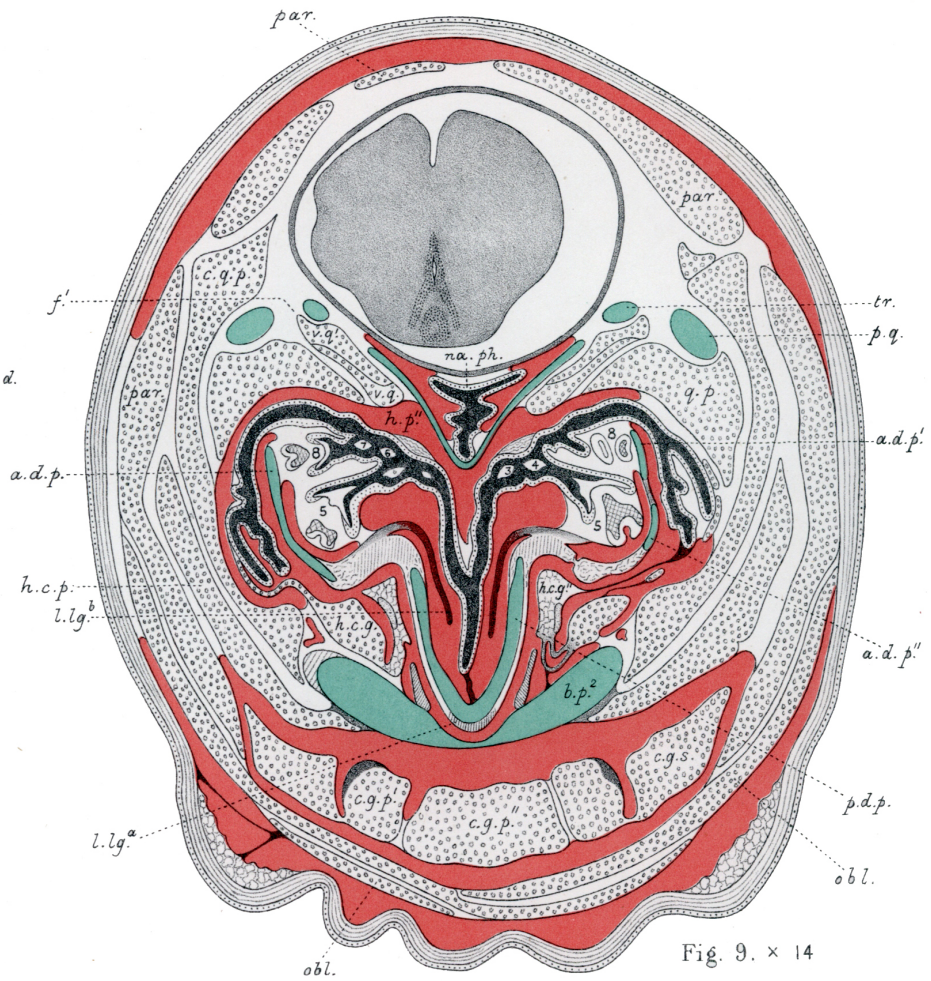

Fig. 9. × 14

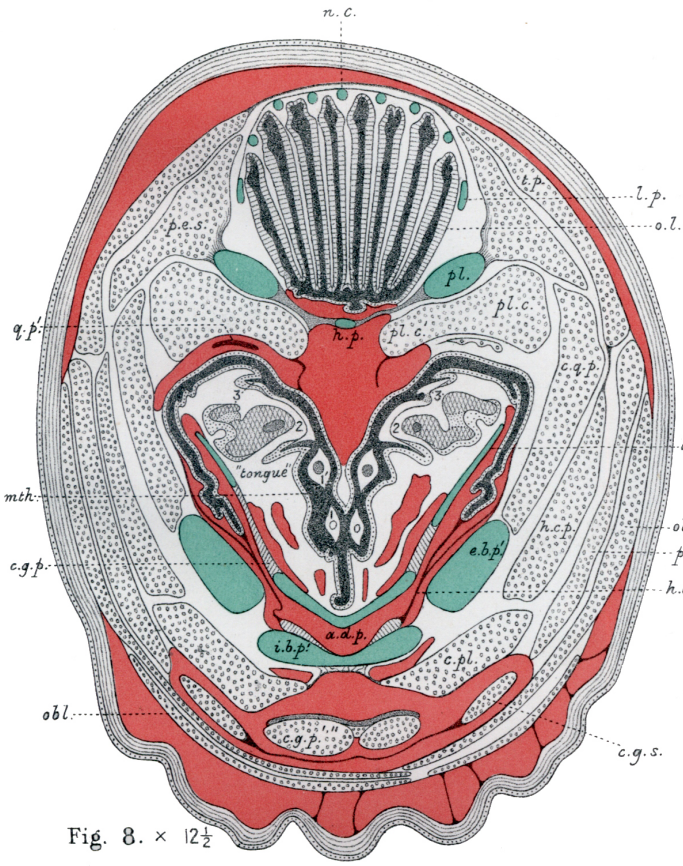

Fig. 8. × 12½

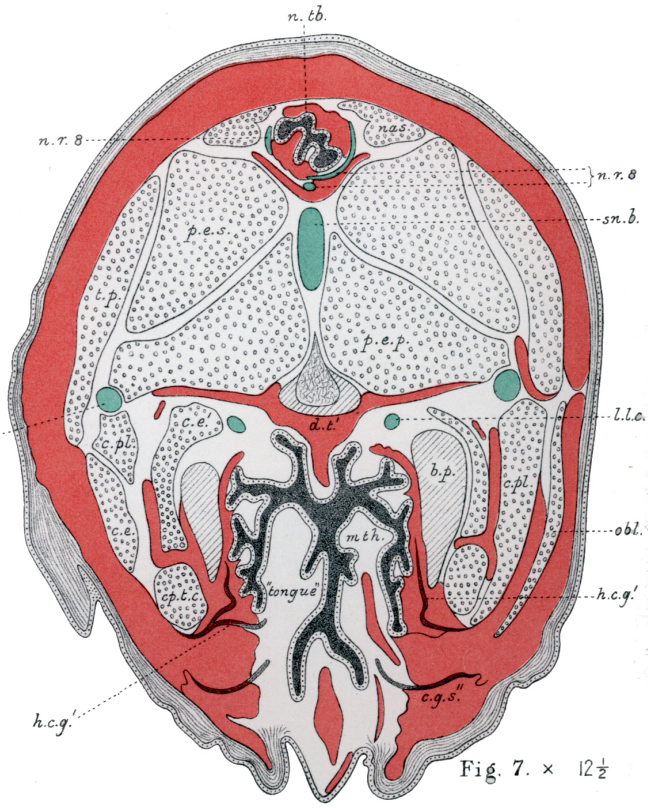

Fig. 7. × 12½

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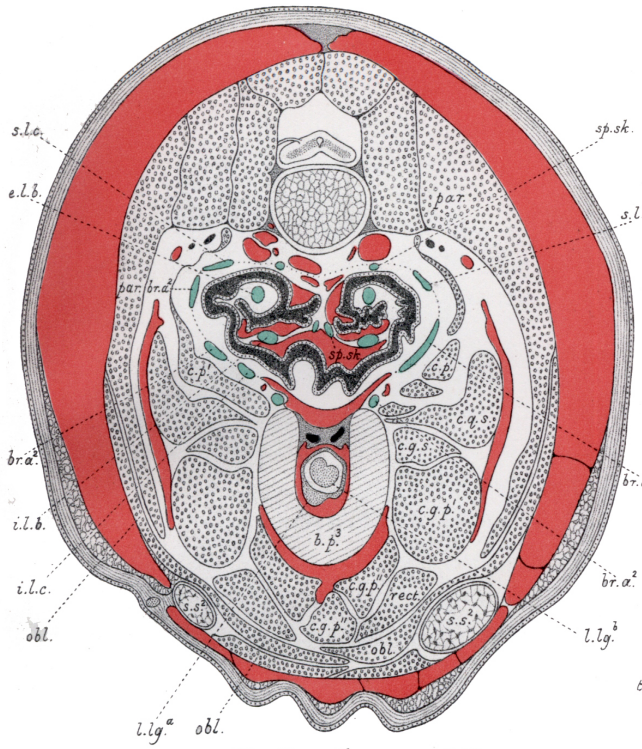

Fig. 11. × 9½ 840

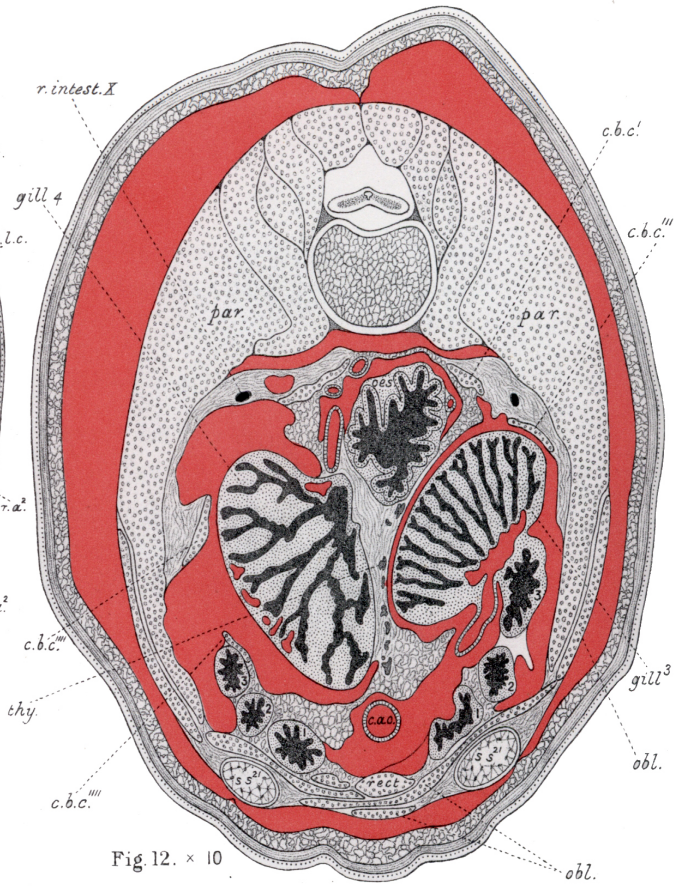

Fig. 12. × 10

2680

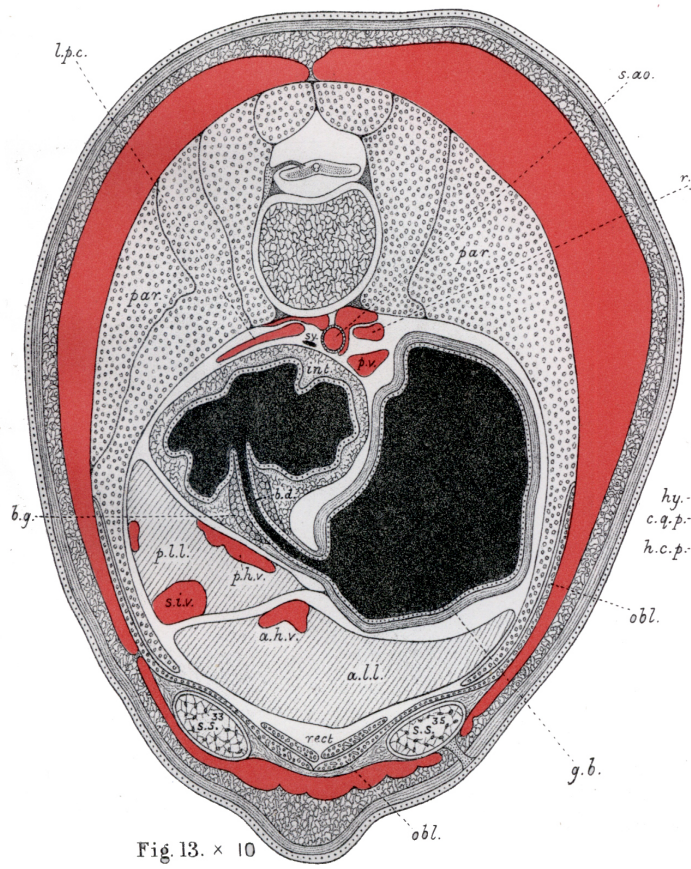

Fig. 13. × 10

3550

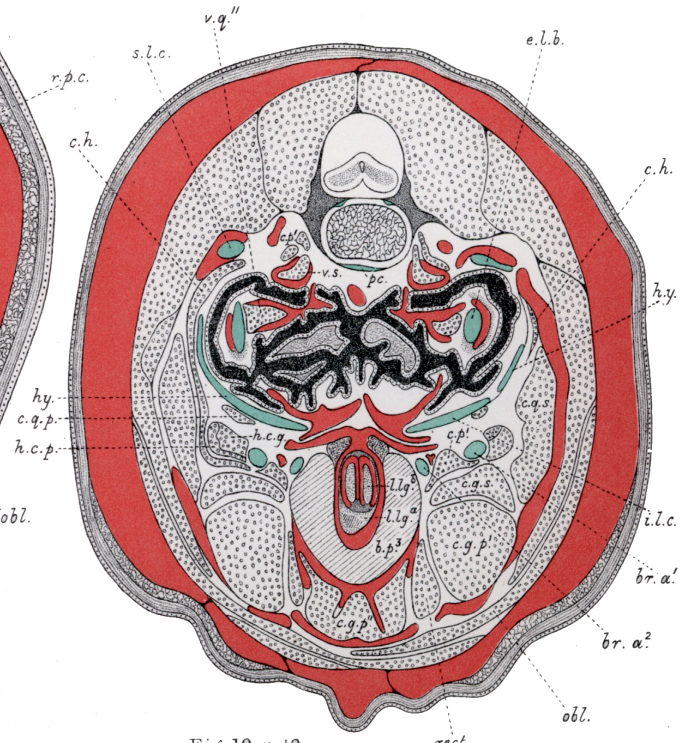

Fig. 10. × 10

720

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