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A MONOGRAPH

ON THE

DEVELOPMENT OF ELASMOBRANCH FISHES.

BY

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PREFACE.

The present Monograph is a reprint of a series of papers published in the *Journal of Anatomy and Physiology* during the years 1876, 1877 and 1878. The successive parts were struck off as they appeared, so that the earlier pages of the work were in print fully two years ago. I trust the reader will find in this fact a sufficient excuse for a certain want of coherence, which is I fear observable, as well as for the omission of references to several recent publications. The first and second chapters would not have appeared in their present form had I been acquainted, at the time of writing them, with the researches which have since been published, on the behaviour of the germinal vesicle and on the division of nuclei. I may also call attention to the valuable papers of Prof. His[1] on the formation of the layers in Elasmobranchs, and of Prof. Kowalevsky[2] on the development of Amphioxus, to both of which I would certainly have referred, had it been possible for me to do so.

Professor His deals mainly with the subjects treated of in Chapter III., and gives a description very similar to my own of the early stages of develop-

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[1] *Zeitschrift f. Anat. u. Entwicklungsgeschichte*, Bd. II.

[2] *Archiv f. Micr. Anat.* Bd. XIII.

ment. His interpretations of the observed changes are, however, very different from those at which I have arrived. Although this is not the place for a discussion of Prof. His's views, I may perhaps state that, in spite of the arguments he has brought forward in support of his position, I am still inclined to maintain the accuracy of my original account. The very striking paper on Amphioxus by Kowalevsky (the substance of which I understand to have been published in Russia at an earlier period) contains a confirmation of the views expressed in Chapter VI. on the development of the mesoblast, and must be regarded as affording a conclusive demonstration, that in the case of Vertebrata the mesoblast has primitively the form of a pair of diverticula from the walls of the archenteron.

The present Memoir, while differing essentially in scope and object from the two important treatises by Professors His[1] and Götte[2], which have recently appeared in Germany, has this much in common with them, that it deals monographically with the development of a single type: but here the resemblance ends. Both of these authors seek to establish, by a careful investigation of the development of a single species, the general plan of development of Vertebrates in general, if not of the whole animal kingdom. Both reject the theory of descent, as propounded by Mr Darwin, and offer completely fresh explanations of the phenomena of Embryology. Accepting, as I do, the principle of natural selection, I have had before me, in writing the Monograph, no such ambitious aim as the

[1] *Erste Anlage des Wirbelthierleibes.*

[2] *Entwicklungsgeschichte der Unke.*

establishment of a completely new system of Morphology. My object will have been fully attained if I have succeeded in adding a few stones to the edifice, the foundations of which were laid by Mr Darwin in his work on the *Origin of Species.*

I may perhaps call attention to one or two special points in this work which seem to give promise of further results. The chapter on the Development of the Spinal and Cranial Nerves contains a modification of the previously accepted views on this subject, which may perhaps lead to a more satisfactory conception of the origin of nerves than has before been possible, and a more accurate account of the origin of the muscle-plates and vertebral column. The attempt to employ the embryological relations of the cephalic prolongations of the body-cavity, and of the cranial nerves, in the solution of the difficult problems of the Morphology of the head, may prove of use in the line of study so successfully cultivated by our great English Anatomist, Professor Huxley. Lastly, I venture to hope that my conclusions in reference to the relations of the sympathetic system and the suprarenal body, and to the development of the mesoblast, the notochord, the limbs, the heart, the venous system, and the excretory organs, are not unworthy of the attention of Morphologists.

The masterly manner in which the systematic position of Elasmobranchs is discussed by Professor Gegenbaur, in the introduction to his Monograph on the Cranial Skeleton of the group, relieves me from the necessity of entering upon this complicated question. It is sufficient for my purpose that the Elasmobranch Fishes be regarded as forming one of the most primitive groups among Vertebrates, a view which finds ample confirmation in the importance of the results to which Prof. Gegenbaur and his pupils have been led in this branch of their investigations.

Though I trust that the necessary references to previous contributions in the same department of enquiry have not been omitted, the 'literature of the subject' will nevertheless be found to occupy a far smaller share of space than is usual in works of a similar character. This is an intentional protest on my part against, what appears to me, the unreasonable amount of space so frequently occupied in this way. The pages devoted to the 'previous literature' only weary the reader, who is not wise enough to skip them, and involve a great and useless expenditure of time on the part of any writer, who is capable of something better than the compilation of abstracts.

In conclusion, my best thanks are due to Drs Dohrn and Eisig for the uniformly kind manner in which they have forwarded my researches both at the Zoological Station in Naples, and after my return to England; and also to Mr Henry Lee and to the Manager and Directors of the Brighton Aquarium, who have always been ready to respond to my numerous demands on their liberality.

To my friend and former teacher Dr Michael Foster I tender my sincerest thanks for the never-failing advice and assistance which he has given throughout the whole course of the work.

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CHAPTER I.

THE RIPE OVARIAN OVUM.

THE ripe ovum is nearly spherical, and, after the removal of its capsule, is found to be unprovided with any form of protecting membrane.

My investigations on the histology of the ripe ovarian ovum have been made with the ova of the Gray Skate (*Raja batis*) only, and owing to a deficiency of material are somewhat imperfect.

The bulk of the ovum is composed of yolk spherules, imbedded in a protoplasmic matrix. Dr Alexander Schultz[1], who has studied with great care the constitution of the yolk, finds, near the centre of the ovum, a kernel of small yolk spherules, which is succeeded by a zone of spherules which gradually increase in size as they approach the surface. But, near the surface, he finds a layer in which they again diminish in size and exhibit numerous transitional forms on the way to molecular yolk-granules. These Dr Schultz regards as in a retrogressive condition.

Another interesting feature about the yolk is the presence in it of a protoplasmic network. Dr Schultz has completely confirmed, and on some points enlarged, my previous observations on this subject[2]. Dr Schultz's confirmation is the more important, since he appears to be unacquainted with my previous investigations. In my paper (*loc. cit.*), after giving a description of the network I make the following statement as to its distribution.

> "A specimen of this kind is represented in Plate XIII. Fig. 2, *n. y*, where the meshes of the network are seen to be finer immediately around the nuclei, and coarser in the intervals. The specimen further shews, in the clearest manner, that this network is not divided into areas, each representing a cell and each containing a nucleus. I do not know to what extent this network extends into

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[1] *Archiv für Micro. Anat.* Vol. XI. 1875.

[2] *Quart. Journ. Micro. Science*, Oct. 1874.

the yolk. I have never yet seen the limits of it, though it is very common to see the coarsest yolk-granules lying in its meshes. Some of these are shewn in Plate XIII. Fig. 2, *y. k.*"

Dr Schultz, by employing special methods of hardening and cutting sections of the whole egg, has been able to shew that this network extends, in the form of fine radial lines, from the centre to the circumference; and he rightly states, that it exhibits no cell-like structures. I have detected this network extending throughout the whole yolk in young eggs, but have failed to see it with the distinctness which Dr Schultz attributes to it in the ripe ovum. Since it is my intention to enter fully both into the structure and meaning of this network in my account of a later stage, I say no more about it here.

At one pole of the ripe ovum a slight examination demonstrates the presence of a small circular spot, sharply distinguished from the remainder of the yolk by its lighter colour. Around this spot is an area which is also of a lighter colour than the yolk, and the outer border of which gradually shades into the normal tint of the yolk. If a section be made through this part (vide Pl. I. fig. 1) the circular spot will be found to be the germinal vesicle, and the area around it a disc of yolk containing smaller spherules than the surrounding parts. The germinal vesicle possessed the same structure in both the ripe eggs examined by me; and, in both, it was situated quite on the external surface of the yolk.

In one of my specimens it was flat above, but convex below; in the other and, on the whole, the better preserved of the two, it had the somewhat quadrangular but rather irregular section represented in Pl. I. fig. 1. It consisted of a thickish membrane and its primitive contents. The membrane surrounded the upper part of the contents and exhibited numerous folds and creases (vide fig. 1). As it extended downwards it became thinner, and completely disappeared at some little distance from the lower end of the contents. These, therefore, rested below on the yolk. At its circumference the membrane of the disc was produced into a kind of fold, forming a rim which rested on the surface of the yolk.

In neither of my specimens is the cavity in the upper part of the membrane filled by the contents; and the upper part of the membrane is so folded and creased that sections through almost any portion of it pass through the folds. The regularity of the surface of the yolk is not broken by the germinal vesicle, and the yolk around exhibits not the slightest signs of displacement. In the germinal vesicle figured the contents are somewhat irregular in shape; but in my other specimen they form a regular mass concave above and convex below. In both cases they rest on the yolk, and the floor of the yolk is exactly moulded to suit the surface of the contents of the germinal vesicle. The contents have a granular aspect, but differ in constitution from the surrounding yolk. Each germinal vesicle measured about one-fiftieth of an inch in diameter.

It does not appear to me possible to suppose that the peculiar appearances which I have drawn and described are to be looked upon as artificial products either of the chromic acid, in which the ova were hardened, or of the instrument with which sections of them were made. It is hardly conceivable that chromic acid could cause a rupture of the membrane and the ejection of the contents of the vesicle. At the same time the uniformity of the appearances in the different sections, the regularity of the whole outline of the egg, and the absence of any signs of disturbance in the yolk, render it impossible to believe that the structures described are due to faults of manipulation during or before the cutting of the sections.

We can only therefore conclude that they represent the real state of the germinal vesicle at this period. No doubt they alone do not supply a sufficient basis for any firm conclusions as to the fate of the germinal vesicle. Still, if they cannot sustain, they unquestionably support certain views. The natural interpretation of them is that the membrane of the germinal vesicle is in the act of commencing to atrophy, preparatory to being extruded from the egg, while the contents of the germinal vesicle are about to be absorbed.

In favour of the extrusion of the membrane rather than its absorption are the following features,

(1) The thickness of its upper surface. (2) The extension of its edge over the yolk. (3) Its position external to the yolk.

In favour of the view that the contents will be left behind and absorbed when the membrane is pushed out, are the following features of my sections:

(1) The rupture of the membrane of the germinal vesicle on its lower surface. (2) The position of the contents almost completely below the membrane of the vesicle and surrounded by yolk.

In connection with this subject, Oellacher's valuable observations upon the behaviour of the germinal vesicle in Osseous Fishes and in Birds at once suggest themselves[1]. Oellacher sums up his results upon the behaviour of the germinal vesicle in Osseous Fishes in the following way (p. 12):

> "The germinal vesicle of the Trout's egg, at a period when the egg is very nearly ripe, lies near the surface of the germinal disc which is aggregated together in a hollow of the yolk....... After this a hole appears in the membrane of the germinal vesicle, which opens into the space between the egg-membrane and the germinal disc. The hole widens more and more, and the membrane frees itself little by little from the contents of the germinal vesicle, which remain behind in the form of a ball on the floor of the cavity formed in this way. The cavity becomes flatter and flatter and the contents are pushed up further and further from the germinal disc. When the hollow, in which lie the contents of the original germinal vesicle, completely vanishes, the covering membrane becomes inverted ......and the membrane is spread out on the convex surface of the germinal disc as a circular, investing structure. It is clear that by the removal of the membrane the contents of the germinal vesicle become lost."

These very definite statements of Oellacher tell strongly against my interpretation of the appearance presented by the germinal vesicle of the ripe Skate's egg. Oellacher's account is so precise, and his drawings so fully bear out his interpretations, that it is very difficult to see where any error can have crept in.

On the other hand, with the exception of those which Oellacher has made, there cannot be said to be any satisfactory observations demonstrating the extrusion of the germinal vesicle from the ovum. Oellacher has observed this definitely for the Trout, but his observations upon the same point in the Bird would quite as well bear the interpretation that the membrane alone became pushed out, as that this occurred to the germinal vesicle, contents and all.

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[1] *Archiv für Micr. Anat.* Vol. VIII. p. 1.

While, then, there are on the one hand Oellacher's observations on a single animal, hitherto unconfirmed, there are on the other very definite observations tending to shew that the germinal vesicle has in many cases an altogether different fate. Götte[1], not to mention other observers before him, has in the case of Batrachian's eggs traced out with great precision the gradual atrophy of the germinal vesicle, and its final absorption into the matter of the ovum.

Götte distinguishes three stages in the degeneration of the germinal vesicle of Bombinator's egg. In the first stage the germinal vesicle has begun to travel up towards the surface of the egg. It retains nearly its primitive condition, but its contents have become more opaque and have partly withdrawn themselves from the thin membrane. The germinal spots are still circular, but in some cases have increased in size. The most important feature of this stage is the smaller size of the germinal vesicle than that of the cavity of the yolk in which it lies, a condition which appears to demonstrate the commencing atrophy of the vesicle.

In the next stage the cavity containing the germinal vesicle has vanished without leaving a trace. The germinal vesicle itself has assumed a lenslike form, and its borders are irregular and pressed in here and there by yolk. Of the membrane of the germinal vesicle, and of the germinal spots, only scanty remnants are to be seen, many of which lie in the immediately adjoining yolk.

In the last stage no further trace of a distinct germinal vesicle is present. In its place is a mass of very finely granular matter, which is without a distinct border and graduates into the surrounding yolk and is to be looked on as a remnant of the germinal vesicle.

This careful investigation of Götte proves beyond a doubt that in Batrachians neither the membrane, nor the contents of the germinal vesicle, are extruded from the egg.

In Mammalia, Van Beneden[2] finds that the germinal vesicle becomes invisible, though he does not consider that it absolutely ceases to exist. He has not traced the steps of the process

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[1] *Entwicklungsgeschichte der Unke.*

[2] *Recherches sur la Composition et la Signification de l'Œuf.*

with the same care as Götte, but it is difficult to believe that an extrusion of the vesicle in the way described by Oellacher would have escaped his notice.

Passing from Vertebrates to Invertebrates, we find that almost every careful investigator has observed the disappearance, apparent or otherwise, of the germinal vesicle, but that very few have watched with care the steps of the process.

The so-called Richtungskörper has been supposed to be the extruded remnant of the germinal vesicle. This view has been especially adopted and supported by Oellacher (*loc. cit.*), and Flemming[1].

The latter author regards the constant presence of this body, and the facility with which it can be stained, as proofs of its connection with the germinal vesicle, which has, however, according to his observations, disappeared before the appearance of the Richtungskörper.

Kleinenberg[2], to whom we are indebted for the most precise observations we possess on the disappearance of the germinal vesicle, gives the following account of it, pp. 41 and 42.

> "We left the germinal vesicle as a vesicle with a distinct doubly contoured membrane, and equally distributed granular contents, in which the germinal spot had appeared......The germinal vesicle reaches 0·06 mm. in diameter, and at the same time its contents undergo a separation. The greater part withdraws itself from the membrane and collects as a dense mass around the germinal spot, while closely adjoining the membrane there remains only a very thin but unbroken lining of the plasmoid material. The intermediate space is filled with a clear fluid, but the layer which lines the membrane retains its connection with the mass around the germinal vesicle by means of numerous fine threads which traverse the space filled with fluid. .....At about the time when the formation of the pseudocells in the egg is completed the germinal spot undergoes a retrogressive metamorphosis, it loses its circular outline and it now appears as if coagulated; then it breaks up into small fragments, and I am fairly confident that these become dissolved. The germinal vesicle...... becomes, on the egg assuming a spherical form, drawn into an eccentric position towards the pole of the egg directed outwards, where it lies close to the surface and only covered by a very thin layer of plasma. In this situation its degeneration now begins, and ends in its complete disappearance. The granular contents become more and more fluid; at the same time part of them pass

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[1] Studien in der Entwicklungsgeschichte der Najaden, *Sitz. d. k. Akad. Wien*, Bd. LXXI. 1875.

[2] *Hydra.* Leipzig, 1872.

out through the membrane. This, which so far was firmly stretched, next collapses to a somewhat egg-like sac, whose wall is thickened and in places folded.

"The inner mass which up to this time has remained compact now breaks up into separate highly refractive bodies, of spherical or angular form and of very different sizes; between them, here and there, are scattered drops of a fluid fat……I am very much inclined to regard the solid bodies in question as fat or as that peculiar modification of albuminoid bodies which we recognise as the certain forerunner of the formation of fat in so many pathologically altered tissues; and therefore to refer the disappearance of the germinal vesicle to a fatty degeneration. On one occasion I believe that I observed an opening in the membrane at this stage; if this is a normal condition it would be possible to believe that its solid contents passed out and were taken up in the surrounding plasma. What becomes of the membrane I am unable to say; in any case the germinal vesicle has vanished to the very last trace before impregnation occurs."

Kleinenberg clearly finds that the germinal vesicle disappears completely before the appearance of the Richtungskörper, in which he states a pseudocell or yolk-sphere is usually found.

The connection between the Richtungskörper and the germinal vesicle is not a result of strict observation, and there can be no question that the evidence in the case of invertebrates tends to prove that the germinal vesicle in no case disappears owing to its extrusion from the egg, but that if part of it is extruded from the egg as Richtungskörper this occurs when its constituents can no longer be distinguished from the remainder of the yolk. This is clearly the case in Hydra, where, as stated above, one of the pseudocells or yolk-spheres is usually found imbedded in the Richtungskörper.

My observations on the Skate tend to shew that, in its case, the membrane of the germinal vesicle is extruded from the egg, though they do not certainly prove this. That conclusion is however supported by the observations of Schenk[1]. He found in the impregnated, but not yet segmented, germinal disc a cavity which, as he suggests, might well have been occupied by the germinal vesicle. It is not unreasonable to suppose that the membrane, being composed of formed matter and able only to take a passive share in vital functions, could, without thereby influencing the constitution of the ovum, be ejected.

If we suppose, and this is not contradicted by observation,

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[1] Die Eier von Raja quadrimaculata, *Sitz. der k. Akad. Wien*, Bd. LXVIII.

that the Richtungskörper is either only the metamorphosed membrane of the germinal vesicle with parts of the yolk, or part of the yolk alone, and assume that in Oellacher's observations only the membrane and not the contents were extruded from the egg, it would be possible to frame a consistent account of the behaviour of the germinal vesicle throughout the animal kingdom, which may be stated in the following way.

The germinal vesicle usually before, but sometimes immediately after impregnation undergoes atrophy and its *contents* become indistinguishable from the remainder of the egg. In those cases in which its membrane is very thick and resistent, *e.g.* Osseous and Elasmobranch Fishes, Birds, etc., this may be incapable of complete resorption, and be extruded bodily from the egg. In the case of most ova, it is completely absorbed, though at a subsequent period it may be extruded from the egg as the Richtungskörper. In all cases the contents of the germinal vesicle remain in the ovum.

In some cases the germinal vesicle is stated to persist and to undergo division during the process of segmentation; but the observations on this point stand in need of confirmation.

My investigations shew that the germinal vesicle atrophies in the Skate before impregnation, and in this respect accord with very many recent observations. Of these the following may be mentioned.

(1) Oellacher (Bird, Osseous Fish). (2) Götte (Bombinator igneus). (3) Kupffer (Ascidia Canina). (4) Strasburger (Phallusia Mamillata). (5) Kleinenberg (Hydra). (6) Metschnikoff (Geryonia, Polyzenia leucostyla, Epibulia aurantiaca, and other Hydrozoa).

This list is sufficient to shew that the disappearance of the germinal vesicle before impregnation is very common, and I am unacquainted with any observations tending to shew that its disappearance is due to impregnation.

In some cases, *e.g.* Asterocanthion[1], the germinal vesicle vanishes after the spermatozoa have begun to surround the egg; but I do not know that its disappearance in these cases has been shewn to be due to impregnation. To do so it would be necessary to prove that in ripe eggs let loose from the ovary, but not fertilized, the germinal vesicle did not undergo the same

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[1] Agassiz, *Embryology of the Star-Fish.*

changes as in the case of fertilized eggs; and this, as far as I know, has not been done. After the disappearance of the germinal vesicle, and before the first act of division, a fresh nucleus frequently appears [—vide—Auerbach (Ascaris nigrovenosa), Fol (Geryonia), Kupffer (Ascidia canina), Strasburger (Phallusia mamillata), Fleming (Anodon), Götte (Bombinator igneus)], which is generally stated to vanish before the appearance of the first furrow; but in some cases (Kupffer and Götte, and as studied with especial care Strasburger) it is stated to divide. Upon the second nucleus, or upon its relation to the germinal vesicle, I have no observations; but it appears to me of great importance to determine whether this fresh nucleus arises absolutely de novo, or is formed out of the matter of the germinal vesicle.

The germinal vesicle is situated in a bed of finely divided yolk-particles. These graduate insensibly into the coarser yolk-spherules around them, though the band of passage between the coarse and the finer yolk-particles is rather narrow. The mass of fine yolk-granules may be called the germinal disc. It is not to be looked upon as diverging in any essential particular from the remainder of the yolk, for the difference between the two is one of degree only. It contains in fact a larger bulk of active protoplasm, as compared with yolk-granules, than does the remainder of the ovum. The existence of this agreement in kind has been already strongly insisted on in my preliminary paper; and Schultz (*loc. cit.*) has arrived at an entirely similar conclusion, from his own independent observations.

One interesting feature about the germinal disc at this period is its size.

My observations upon it have been made with the eggs of the Skate (Raja) alone; but I think that it is not probable that its size in the Skate is greater than in Scyllium or Pristiurus. If its size is the same in all these genera, then the germinal disc of the unimpregnated ovum is very much greater than that portion of the ovum which undergoes segmentation, and which is usually spoken of as the germinal disc in impregnated ova.

I have no further observation on the ripe ovarian ovum; and my next observations concern an ovum in which two furrows have already appeared.

CHAPTER II.

THE SEGMENTATION.

I HAVE not been fortunate enough to obtain an absolutely complete series of eggs during segmentation.

In the cases of Pristiurus and Scyllium only have I had any considerable number of eggs in this condition, though one or two eggs of Raja in which the process was not completed have come into my hands.

In the youngest impregnated Pristiurus eggs, which I have obtained, the germinal disc was already divided into four segments.

The external appearance of the blastoderm, which remains nearly constant during segmentation, has been already well described by Leydig[1].

The yolk has a pale greenish tinge which, on exposure to the air, acquires a yellower hue. The true germinal disc appears as a circular spot of a bright orange colour, and is, according to Leydig's measurements, 1½ m. in diameter. Its colour renders it very conspicuous, a feature which is further increased by its being surrounded by a narrow dark line (Pl. I. fig. 2), the indication of a shallow groove. Surrounding this line is a concentric space which is lighter in colour than the remainder of the yolk, but whose outer border passes by insensible gradations into the yolk. As was mentioned in my preliminary paper (*loc. cit.*), and as Leydig (*loc. cit.*) had before noticed, the germinal disc is always situated at the pole of the yolk which is near the rounded end of the Pristiurus egg. It occupies a corresponding position in the eggs of both species of Scyllium (stellare and canicula) near the narrower end of the egg to which the shorter pair of strings is attached. The germinal disc in the youngest egg examined, exhibited two furrows which

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[1] *Rochen und Haie.*

crossed each other at right angles in the centre of the disc, but neither of which reached its edge. These furrows accordingly divided the disc into four segments, completely separated from each other at the centre of the disc, but united near its circumference.

I made sections, though not very satisfactorily, of this germinal disc. The sections shewed that the disc was composed of a protoplasmic basis, in which were imbedded innumerable minute spherical yolk-globules so closely packed as to constitute nearly the whole mass of the germinal disc.

In passing from the coarsest yolk-spheres to the fine spherules of the germinal disc, three bands of different-sized yolk-particles have to be traversed. These bands graduate into one another and are without sharp lines of demarcation. The outer of the three is composed of the largest-sized yolk-spherules which constitute the greater part of the ovum. The middle band forms a concentric layer around the germinal disc, and is composed of yolk-spheres considerably smaller than those outside it. Where it cuts the surface it forms the zone of lighter colour immediately surrounding the germinal disc. The innermost band is formed by the germinal disc itself and is composed of spherules of the smallest size. These features are shewn in Pl. I. fig. 6, which is the section of a germinal disc with twenty-one segments; in it however the outermost band of spherules is not present.

From this description it is clear, as has already been mentioned in the description of the ripe unimpregnated ovum, that the germinal disc is not to be looked upon as a body entirely distinct from the remainder of the ovum, but merely as a part of the ovum in which the protoplasm is more concentrated and the yolk-spherules smaller than elsewhere. Sections shew that the furrows visible on the surface end below, as indeed they do on the surface, before they reach the external limit of the finely granular matter of the germinal disc. There are therefore at this stage no distinct segments: the otherwise intact germinal disc is merely grooved by two furrows.

I failed to observe any nuclei in the germinal disc just described, but it by no means follows that they were not present.

In the next youngest of the eggs[1] examined the germinal disc was already divided into twenty-one segments. When viewed from the surface (Pl. I. fig. 3), the segments appeared divided into two distinct groups—an inner group of eleven smaller segments, and an outer group of segments surrounding the former. The segments of both the inner and the outer group were very irregular in shape and varied considerably in size. The amount of irregularity is far from constant and many germinal discs are more regular than the one figured.

In this case the situation of the germinal disc and its relations to the yolk were precisely the same as in the earlier stage.

In sections of this germinal disc (Pl. I. fig. 6), the groove which separates it from the yolk is well marked on one side, but hardly visible at the other extremity of the section.

Passing from the external features of this stage to those which are displayed by sections, the striking point to be noticed is the persisting continuity of the segments, marked out on the surface, with the floor of the germinal disc.

The furrows which are visible on the surface merely form a pattern, but do not isolate a series of distinct segments. They do not even extend to the limit of the finely granular matter of the germinal disc.

The section represented, Pl. I. fig. 6, bears out the statements about the segments as seen on the surface. There are three smaller segments in the middle of the section, and two larger at the two ends. These latter are continuous with the coarser yolk-spheres surrounding the germinal disc and are not separated from them by a segmentation furrow.

In a slightly older embryo than the one figured I met with a few completely isolated segments at the surface. These segments were formed by the apparent bifurcation of furrows as they neared the surface of the germinal disc. The segments thus produced are triangular in form. They probably owe their origin to the meeting of two oblique furrows. The last-formed of these furrows apparently ceases to be prolonged after meeting the first-formed furrow. I have not in any case observed an example of two furrows crossing one another at this stage.

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[1] The germinal disc figured was from the egg of a Scyllium stellare and not Pristiurus, but I have also sections of a Pristiurus egg of the same age, which do not differ materially from the Scyllium sections.

The furrows themselves for the most part are by no means simple slits with parallel sides. They exhibit a beaded structure, shewn imperfectly in Pl. I. fig. 6, but better in Pl. I. fig. 6 *a*, which is executed on a larger scale. They present intervals of dilatations where the protoplasms of the segments on the two sides of the furrow are widely separated, alternating with intervals where the protoplasms of the two segments are almost in contact and are only separated from one another by a very narrow space.

A closer study of the germinal disc at this period shews that the cavities which cause the beaded structure of the furrows are not only present along the lines of the furrows but are also found scattered generally through the germinal disc, though far more thickly in the neighbourhood of the furrows. Their appearance is that of vacuoles, and with these they are probably to be compared. There can be little question that in the living germinal disc they are filled with fluid. In some cases, they are collected in very large numbers in the region of a furrow. Such a case as this is shewn in Pl. I. fig. 6 *b*. In numerous other cases they occur, roughly speaking, alternately on each side of a furrow. Some furrows, though not many, are entirely destitute of these structures. The character of their distribution renders it impossible to overlook the fact that these vacuole-like bodies have important relations with the formation of the segmentation furrows.

Lining the two sides of the segmentation furrows there is present in sections a layer which stains deeply with colouring re-agents; and the surface of the blastoderm is stained in the same manner. In neither case is it permissible to suppose that any membrane-like structure is present. In many cases a similar very delicate, but deeply-stained line, invests the vacuolar cavities, but the fluid filling these remains quite unstained. When distinct segments are formed, each of these is surrounded by a similarly stained line.

The yolk-spherules are so numerous, and render even the thinnest section so opaque, that I have failed to make satisfactory observations on the behaviour of the nucleus. I find nuclei in many of the segments, though it is very difficult even to see them, and only in very favourable specimens can their structure be studied. In some cases, two of them lie one on each side of a furrow; and in one case at the extreme end of a furrow I could see two peculiar aggregations of yolk-spherules united by a band through which the furrow, had it been continued, would have passed. The connection (if any exists) between this appearance and the formation of the fresh nuclei in the segments, I have been unable to elucidate.

The peculiar appearances attending the formation of fresh nuclei in connection with cell-division, which have recently been described by so many observers, have hitherto escaped my observation at this stage of the segmentation, though I shall describe them in a later stage. A nucleus of this stage is shewn on Pl. I. fig. 6 *c*. It is lobate in form and is divided by lines into areas in each of which a deeply-stained granule is situated.

The succeeding stages of segmentation present from the surface no fresh features of great interest. The somewhat irregular (Pl. I. figs. 4 and 5) circular line, which divides the peripheral larger from the central smaller segments, remains for a long time conspicuous. It appears to be the representative of the horizontal furrow which, in the Batrachian ovum, separates the smaller pigmented spheres from the larger spheres of the lower pole of the egg.

As the segments become smaller and smaller, the distinction between the peripheral and the central segments becomes less and less marked; but it has not disappeared by the time that the segments become too small to be seen with the simple lens. When the spheres become smaller than in the germinal disc represented on Pl. I. fig. 5, the features of segmentation can be more easily and more satisfactorily studied by means of sections.

To the features presented in sections, both of the latter and of the earlier blastoderms, I now return. A section of one of the earlier germinal discs, of about the age of the one represented on Pl. I. fig. 4, is shewn in Pl. II. fig. 7.

It is clear at a glance that we are now dealing with true segments completely circumscribed on all sides. The peripheral segments are, as a rule, larger than the more central ones, though in this respect there is considerable irregularity.

The segments are becoming smaller by repeated division; but, in addition to this mode of increase, there is now going on outside the germinal disc a segmentation of the yolk, by which fresh segments are being formed from the yolk and added to those which already exist in the germinal disc. One or two such segments are seen in the act of being formed (Pl. II. fig. 7 *f*); and it is to be noticed that the furrows which will eventually mark out the segments, do so at first in a partial manner only, and do not circumscribe the whole circumference of the segment in the act of being formed. These fresh furrows are thus repetitions on a small scale of the earliest segmentation furrows.

It deserves to be noticed that the portion of the germinal disc which has already undergone segmentation, is still surrounded by a broad band of small-sized yolk-spherules. It appears to me probable that owing to changes taking place in the spherules of the yolk, which result in the formation of fresh spherules of a small size, this band undergoes a continuous renovation.

The uppermost row of segmentation spheres is now commencing to be distinguished from the remainder as a separate layer which becomes progressively more distinct as segmentation proceeds.

The largest segments in this section measure about the $\frac{1}{100}$th of an inch in diameter, and the smallest about $\frac{1}{300}$th of an inch.

The nuclei at this stage present points of rather a special interest. In the first place, though visible in many, and certainly present in all the segments[1], they are not confined to these: they are also to be seen, in small numbers, in the band of fine spherules which surrounds the already segmented part of the germinal disc. Those found outside the germinal disc are not confined to the spots where fresh segments are appearing, but are also to be seen in places where there are no traces of fresh segments.

This fact, especially when taken in connection with the forma-

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[1] In the figure of this stage, I have inserted nuclei in all the segments. In the section from which the figure was taken, nuclei were not to be seen in many of the segments, but I have not a question that they were present in all of them. The difficulty of seeing them is, in part, due to the yolk-spherules and in part to the thinness of the section as compared with the diameter of a segmentation sphere.

tion of fresh segments outside the germinal disc and with other facts which I shall mention hereafter, is of great morphological interest as bearing upon the nature and homologies of the food-yolk. It also throws light upon the behaviour and mode of increase of the nuclei. All the nuclei, both those of the segments and those of the yolk, have the peculiar structure I described in the last stage.

In specimens of this stage I have been able to observe certain points which have an important bearing upon the behaviour of the nucleus during cell-division.

Three figures, illustrating the behaviour of the nucleus, as I have seen it in sections of blastoderms hardened in chromic acid, are shewn in Pl. II. figs. 7*a*, 7*b* and 7*c*.

In the place of the nucleus is to be seen a sharply defined figure (Fig. 7 *a*) stained in the same way as the nucleus or more deeply. It has the shape of two cones placed base to base. From the apex of each cone there diverge towards the base a series of excessively fine striæ. At the junction between the two cones is an irregular linear series of small deeply stained granules which form an apparent break between the two. The line of this break is continued very indistinctly beyond the edge of the figure on each side.

From the apex of each cone there diverge outwards into the protoplasm of the cell a series of indistinct markings. They are rendered obscure by the presence of yolk-spherules, which completely surround the body just described, but which are not arranged with any reference to these markings. These latter striæ, diverging from the apex of the cone, are more distinctly seen when the apex points to the observer (Fig. 7 *b*), than when a side of the cone is in view.

The striæ diverging outwards from the apices of the cones must be carefully distinguished from the striæ of the cones themselves. The cones are bodies quite as distinctly differentiated from the protoplasm of the cell as nuclei, while the striæ which diverge from their apices are merely structures in the general protoplasm of the cell.

In some cells, which contain these bodies, no trace of a commencing line of division is visible. In other cases (Fig. 7 *c*), such a line of division does appear and passes through the junction of the two cones. In one case of this kind I fancied I could see (and have represented) a coloured circular body in each cone. I do not feel any confidence that these two bodies are constantly present; and even where visible they are very indistinct.

Instead of an ordinary nucleus a very indistinctly marked vesicular body sometimes appears in a segment; but whether it is to be looked on as a nucleus not satisfactorily stained, or as a nucleus in the act of being formed, I cannot decide.

With reference to the situation of the cone-like bodies I have described I have made an observation which appears to me to be of some interest. I find that bodies of this kind are found in the yolk *completely outside* the germinal disc. I have made this observation, in at least two cases which admitted of no doubt (vide Fig. 7 *nx'*).

We have therefore the remarkable fact, that whatever connection these bodies may have with cell-division, they can occur in cases where this is altogether out of the question and where an increase in the number of nuclei can be their only product.

These are the main facts which I have been able to determine with reference to the nuclei of this stage; but it will conduce to clearness if I now finish what I have to say upon this subject.

At a still later stage of segmentation the same peculiar bodies are to be seen as during the stage just described, but they are rarer; and, in addition to them, other bodies are to be seen of a character intermediate between ordinary nuclei and the former bodies.

Three such are represented in Pl. II. figs. 8 *a*, 8 *b*, 8 *c*. In all of these there can be traced out the two cones, which are however very irregular. The striation of the cones is still present, but is not nearly so clear as it was in the earlier stage.

In addition to this, there are numerous deeply stained granules scattered about the two figures which resemble exactly the granules of typical nuclei.

All these bodies occupy the place of an ordinary nucleus, they stain like an ordinary nucleus and are as sharply defined as an ordinary nucleus.

There is present around some of these, especially those situated in the yolk, the network of lines of the yolk described by me in a preliminary paper[1], and I feel satisfied that there is in some cases an actual connection between the network and the nuclei. This network I shall describe more fully hereafter.

Further points about these figures and the nuclei of this stage I should like to have been able to observe more completely than I have done, but they are so small that with the highest powers I possess (Zeiss, Immersion No. $2 = \frac{1}{15}$ in.) their complete and satisfactory investigation is not possible.

Most of the true nuclei of the cells of the germinal disc are regularly rounded; those however of the yolk are frequently irregular in shape and often provided with knob-like processes. The gradations are so complete between typical nuclei and bodies like that shewn (Pl. II. fig. 8 *c*) that it is impossible to refuse the name of nucleus to the latter.

In many cases *two nuclei* are present in one cell.

In later stages knob-like nuclei of various sizes are scattered in very great numbers in the yolk around the blastoderm (vide Pl. III. IV. V.). In some cases it appears to me that several of these are in close juxta-position, as if they had been produced by the division of one primitive nucleus. I do not feel absolutely confident that this is the case, owing to the fact that in the investigation of a knobbed body there is great difficulty in ascertaining that the knobs, which appear separate in one plane, are not in reality united in another.

I have, in spite of careful search, hitherto failed to find amongst these later nuclei cone-like figures, similar to those I found in the yolk during segmentation. This is the more remarkable since in the early stages of segmentation, when very few nuclei are present in the yolk, the cone-like figures are not uncommon; whereas, in the latter stages of development when the nuclei of the yolk are very common and obviously increasing rapidly, such figures are not to be met with.

In no case have I been able to see a distinct membrane round any of the nuclei.

I have hitherto attempted to describe the appearances

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[1] *Loc. cit.*

bearing on the behaviour of the nuclei in as objective a manner as possible.

My observations are not as complete as could be desired; but, taken in conjunction with those of other investigators, they appear to me to point towards certain definite conclusions with reference to the behaviour of the nucleus in cell-division.

The most important of these conclusions may be stated as follows. In the act of cell-division the nuclei of the resulting cells are formed from the nucleus of the primitive cell.

This may occur;—

(1) By the complete solution of the old nucleus within the protoplasm of the mother cell and the subsequent reaggregation of its matter to form the nuclei of the freshly formed daughter cells,

(2) By the simple division of the nucleus,

(3) Or by a process intermediate between these two where part of the old nucleus passes into the general protoplasm and part remains always distinguishable and divides; the fresh nucleus being in this case formed from the divided parts as well as from the dissolved parts of the old nucleus.

Included in this third process it is permissible to suppose that we may have a series of all possible gradations between the extreme processes 1 and 2. If it be admitted, and the evidence we have is certainly in favour of it, that in some cases, both in animal and vegetable cells, the nucleus itself divides during cell-division, and in others the nucleus completely vanishes during the cell-division, it is more reasonable to suspect the existence of some connection between the two processes, than to suppose that they are entirely different in kind. Such a connection is given by the hypothesis I have just proposed.

The evidence for this view, derived both from my own observations and those of other investigators, may be put as follows.

The absolute division of the nucleus has been stated to occur in animal cells, but the number of instances where the evidence is quite conclusive are not very numerous. Recently F. E. Schultze[1] appears to have observed it in the case of an Amœba in an altogether satisfactory manner. The instance is

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[1] *Archiv f. Micr. Anat.* XI. p. 592.

quoted by Flemming[1]. Schultze saw the nucleus assume a dumb-bell shape, divide, and the two halves collect themselves together. The whole process occupied a minute and a half and was shortly followed by the division of the Amœba, which occupied eight minutes. Amongst vegetable cells the division of the nucleus seems to be still rarer than with animal cells. Sachs[2] admits the division of the nucleus in the case of the parenchyma cells of certain Dicotyledons (Sambucus, Helianthus, Lysimachia, Polygonum, Silene) on the authority of Hanstein.

The division of the nucleus during cell-division, though seemingly not very common, must therefore be considered as a thoroughly well authenticated occurrence.

The frequent disappearance of the nucleus during cell-division is now so thoroughly recognised, both for animal and vegetable cells, as to require no further mention.

In many cases the partial or complete disappearance of the nucleus is accompanied by the formation of two peculiar star-like figures. Appearances of the kind have been described by Fol[3], Flemming[4], Auerbach[5] and possibly also Oellacher[6] as well as other observers.

These figures[7] are possibly due to the streaming out of the protoplasm of the nucleus into that of the cell[8]. The

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[1] *Entwicklungsgeschichte der Najaden*, LXXI. Bd. der *Sitz. der k. Akad. Wien*, 1875.

[2] *Text-Book of Botany*, English trans. p. 19.

[3] *Entw. d. Geryonideneies. Jenaische Zeitschrift*, Bd. VII.

[4] *Loc. cit.*

[5] *Organologische Studien*, Zweites Heft.

[6] *Beiträge z. Entwicklungsgeschichte der Knochenfischen: Zeit. für Wiss. Zoologie.* Bd. XXII. 1872.

[7] The memoirs of Auerbach and Strasburger (*Zellbildung u. Zelltheilung*) have unfortunately come into my hands too late for me to take advantage of them. Especially in the magnificent monograph of Strasburger I find drawings precisely resembling those from my specimens already in the hands of the engraver. Strasburger comes to the conclusion from his investigations that the modified nucleus always divides and never vanishes as is usually stated. If his views on this point are correct part of the hypothesis I have suggested above is rendered unnecessary. The striæ of the protoplasm, which in accordance with Auerbach's view I have considered as being due to a streaming out of the matter of the nucleus, he regards as resulting from a polarity of the particles in the cell and the attraction of the nucleus. My own investigations though, as far as they go, quite in accordance with those of Strasburger, do not supply any grounds for deciding on the meaning of these striæ; and in some respects they support Strasburger's views against those of other observers, since they demonstrate that in Elasmobranchs the modified nucleus does actually divide.

[8] This is the view which has been taken by Auerbach (*Organologische Studien*).

appearance of striation may on this hypothesis be explained as due to the presence of granules in the protoplasm. When the streaming out of the protoplasm of a nucleus into that of a cell takes place, any large granule which cannot be moved by the stream will leave behind it a slack area where there is no movement of the fluid. Any granules which are carried into this area will remain there, and by the continuation of a process of this kind a row of granules may be formed, and a series of such rows would produce an appearance of striation. In many cases, *e.g.* Anodon, vide Flemming[1], even the larger yolk-spherules are arranged in this fashion.

On the supposition that the striation of these figures is due to the outflow from the nucleus, the appearances presented in Elasmobranchs admit of the following explanation.

The central body consisting of two cones (Figs. 7*a*, 7*c*) is almost without question the remnant of the primitive nucleus. This is shewn by its occupying the same position as the primitive nucleus, staining in the same way, and by there being a series of insensible gradations between it and a typical nucleus. The contents must be supposed to be streaming out from the two apices of the cones, as appears from the striæ in the body converging on each side towards the apex, and then diverging again from it. In my specimens the yolk-spherules are not arranged with any reference to the radiating striation.

It is very likely that in the cases of the disappearance of the nucleus, its protoplasm streams out in two directions, towards the two parts of the cell which will eventually become separated from each other; and probably, after the division, the matter of the old nucleus is again collected to form two fresh nuclei.

In some cases of cell-division a remnant of the old nucleus is stated to be visible after the fresh nuclei have appeared. These cases, of which I have not seen full accounts, are perhaps analogous to what occasionally happens with the germinal vesicle of an ovum. The whole of the contents of the germinal vesicle become at its disappearance mingled with the protoplasm of the ovum, but the resistent membrane remains and is eventually ejected from the egg, vide p. 3 *et seq.* If the

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[1] *Loc. cit.*

remnant of the old nucleus in the cases described is nothing more than its membrane, no difficulty is offered to the view that the constituents of the old nucleus may help to form the new ones.

In many cases the total bulk of the new nuclei is greater than that of the old one; in such instances part of the protoplasm of the cell necessarily has a share in forming the new nuclei.

Although, in instances where the nucleus vanishes, an absolute demonstration of the formation of the fresh nuclei from the matter of the old one is not possible; yet, if cases of the division of the old nucleus to form the new ones be admitted to exist, the derivation in the first process of the fresh nuclei from the old ones must be postulated in order to maintain a continuity between the two processes of formation; and, as I have attempted to shew, all the circumstantial evidence is in favour of it.

Admitting the existence of the two extreme processes of nuclear formation, I wish to shew that my results in Elasmobranchs tend to demonstrate the existence of intermediate steps between them. The first figures I described of two opposed cones, appear to me almost certainly to represent nuclei in the act of dissolution; but though a portion of the nucleus may stream out into the yolk, I think it impossible that the whole of it does[1].

I described these bodies in two states. An earlier one, in which the two cones were separated by an irregular row of deeply stained granules; and a later one in which a furrow had already appeared dividing the cones as well as the cell. In neither of these conditions could I see any signs of the body vanishing completely. It was as clearly defined and as deeply stained as an ordinary nucleus, and in its later condition the signs of the streaming out of material from its pointed extremities were less marked than in the earlier stage.

All these facts, to my mind, point to the view that these cone-like bodies do not disappear, but form the basis for the new nuclei. Possibly the body visible in each cone

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[1] After Strasburger's observation it must be considered very doubtful whether the streaming out of the contents of the nucleus, in the manner implied in the text, really takes place.

in the later stage, was the commencement of this new nucleus. Götte[1] has figured structures somewhat similar to these bodies, but I hardly understand either his figure or his account sufficiently clearly to be able to pronounce upon the identity of the two. In case they are identical, Götte gives a very different explanation of them from my own[2].

A second of my results, which points to a series of intermediate steps between division and solution of the nucleus, is the distribution in time of the peculiar cone-like bodies. These are present in fair abundance at an early period of segmentation, when there are but few nuclei either in the blastoderm or the yolk. But at later periods, when there are both more nuclei, especially in the yolk, and they are also increasing in numbers more rapidly than before, no bodies of this kind are to be seen. This fact becomes the more striking from the lobate appearance of the later nuclei of the yolk, an appearance which exactly suits the hypothesis of the rapid budding off of fresh nuclei.

The observations of R. Hertwig[3] on the gemmation of *Podophrya Gemmipara*, support my interpretation of the knobbed condition of the nuclei. Hertwig finds (p. 47) that

> The horse-shoe shaped nucleus grows out into numerous anastomosing projections. Over the free ends of the projections little knobs appear on the surface of the body, into which the lengthening ends of the processes of the nucleus grow up. Here they bend themselves into a horse-shoe form. The newly-formed nucleus then separates from the original nucleus, and afterwards the bud containing it from the body.

From the peculiar arrangement of the net-work of lines of the yolk around these knobbed nuclei, it is reasonable to conclude that interchange of material between the protoplasm of the yolk and the nuclei is still taking place, even during the later periods.

These facts about the distribution in time of the cone-like

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[1] *Entwicklungsgeschichte der Unke*, Pl. I. fig. 18.

[2] As I before mentioned, Strasburger (*Zellbildung u. Zelltheilung*) has represented bodies precisely similar to those I have described, which appear during the segmentation in the egg of *Phallusia Mammillata* as well as similar figures observed by Butschli in eggs of *Cucullanus elegans* and *Blatta Germanica*. The figures in this monograph are the only ones I have seen, which are identical with my own.

[3] *Morphologisches Jahrbuch*, Bd. I. pp. 46, 47.

bodies afford a strong presumptive evidence of a change in the manner of nuclear increase.

The last argument I propose urging on this head is derived from the bodies (Pl. II. fig. 8 *a*, *b*, *c*) which I have described as intermediate between the true cone-like bodies and typical nuclei. They appear to afford evidence of less and less of the matter of the nucleus streaming out into the yolk and of a large proportion of it becoming divided.

The conclusion to be derived from all these facts is that for Elasmobranchs in the earlier stages of segmentation, and during the formation of fresh segments, a partial solution of the old nucleus takes place, but all its constituents serve for the reconstruction of the fresh nuclei.

In later periods of development a still smaller part of the nucleus becomes dissolved, and the rest divides; but the two fresh nuclei are still derived from the two sources. After the close of segmentation the fresh nuclei are formed by a simple division of the older ones.

The appearance of the cone-like bodies in the yolk outside the germinal disc is a point of some interest. It demonstrates in a conclusive manner that whatever influence (if any) the nucleus may have in ordinary cases of cell division, yet it may undergo changes of a precisely similar character to those which it experiences during cell division, without exerting any influence on the surrounding protoplasm[1]. If the lobate nuclei are also nuclei undergoing division, we have in the egg of an Elasmobranch examples of all the known forms of nuclear increase unaccompanied by cell division.

The next stage in the segmentation does not present so many features of interest as the last one. The segments are now so small, as to be barely visible from the surface with a simple lens. A section of an embryo of this stage is represented in Pl. II. fig. 8. The section, which is drawn on the

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[1] Strasburger's (*loc. cit.*) arguments about the influence of the nucleus in cell division are not to my mind conclusive; though not without importance. It is difficult to reconcile his views with the facts of cell division observable during the Elasmobranch segmentation; but even if their truth be admitted they do not bring us much nearer to a satisfactory understanding of cell division, unless accompanied (and at present they are not so) by a rational explanation of the forces which produce the division of the nucleus.

same scale as the section belonging to the last stage, serves to shew the relative size of the segments in the two cases.

The epiblast is now more distinct than it was. The segments composing it are markedly smaller than the remainder of the cells of the germinal disc, but possess nuclei of an absolutely larger size than do the other cells. They are irregular in shape, with a slight tendency to be columnar. An average segment of this layer measures about $\frac{1}{700}$ inch.

The cells of the lower layer are more polygonal than those of the epiblast, and are decidedly larger. An average specimen of the larger cells of the lower layer measures about $\frac{1}{400}$ in. in diameter, and is therefore considerably smaller than one of the smallest cells of the last stage. The formation of fresh segments from the yolk still continues with fair rapidity, but nearly comes to an end shortly after this.

Of the nuclei of the lower layer cells, there is not much to add to what has already been said. Not infrequently two nuclei may be observed in a single cell.

The nuclei in the yolk which surrounds the germinal disc are more numerous than in the earlier periods, and are now to be met with in fair numbers in every section (Fig. 8 *n*′).

These are the main features which characterise the present stage, they are in all essential points similar to those of the last stage, and the two germinal discs hardly differ except in the size of the segments of which they are composed.

In the last stage which I consider as belonging to the segmentation, the cells of the whole blastoderm have become smaller (Pl. II. fig. 9).

The epiblast (*ep*) now consists of a very marked layer of columnar cells. It is, as far as I have been able to observe, never more than one cell deep. The cells of the lower layer are of an approximately uniform size, though a few of those at the circumference of the blastoderm considerably exceed the remainder in the bulk.

There are two fresh features of importance in germinal discs of this age.

Instead of being but indistinctly separated from the surrounding yolk, the blastoderm has now very clearly defined limits.

This is an especially marked feature of preparations made with osmic acid. In these there may frequently be seen a deeply stained doubly contoured line, which forms the limit of the yolk, where it surrounds the germinal disc. Lines of this kind are often to be seen on the surface of the yolk, or even of the blastoderm, but are probably to be regarded as products of reagents, rather than as organised structures. The outline of the germinal disc is well rounded, though it is occasionally broken, from the presence of a larger cell in the act of being formed from the yolk.

It is not probable that any great importance is to be attached to the comparative distinctness of the outline of the germinal disc at this stage, which is in a great measure due to a cessation in the formation of fresh cells in the surrounding yolk, and in part to the small and comparatively uniform size of the cells of the germinal disc.

The formation of fresh cells from the yolk nearly comes to an end during this period, but it still continues on a small scale.

The number of the nuclei around the germinal disc has increased.

Another feature of interest which first becomes apparent during this stage is the asymmetry of the germinal disc. If a section were made through the germinal disc, as it lay *in situ* in the egg capsule, parallel or nearly so to the long axis of the capsule, one end of the section would be found to be much thicker than the other. There would in fact be a far larger collection of cells at one extremity of the germinal disc than at the other. The end at which this collection of cells is formed points towards the end of the egg capsule opposite to that near which the yolk is situated. This collection of cells is the first trace of the embryo; and with its appearance the segmentation may be supposed to terminate.

The section I have represented, though not quite parallel to the long axis of the egg, is sufficiently nearly so to shew the greater mass of cells at the embryonic end of the germinal disc.

This very early appearance of a distinction in the germinal disc between the extremity at which the embryo appears and the non-embryonic part of the disc, besides its inherent interest, has a further importance from the fact that in Osseous Fishes a similar occurrence takes place. Oellacher[1] and Götte[2] both agree as to the very early period at which a thickening of one extremity of the blastoderm in Osseous Fishes is formed, which serves to indicate the position at which the embryo will appear. There are many details of development in which Osseous Fish and Elasmobranchs agree, which, although if taken individually are without any great importance, yet serve to shew how long even insignificant features in development may be retained.

The segmentation of the Elasmobranch egg presents in most of its features great regularity, and exhibits in its mode of occurrence the closest resemblance to that in other meroblastic vertebrate ova.

There is, nevertheless, one point with reference to which a slight irregularity may be observed. In almost all eggs segmentation commences by, what for convenience may be called, a vertical furrow which is followed by a second vertical furrow at right angles to the first. The third furrow however is a horizontal one, and cuts the other two at right angles. This method of segmentation must be looked on as the normal one, in almost all the important groups of the animal kingdom, both for the so-called holoblastic and meroblastic eggs, and the gradations intermediate between the two. The Frog amongst vertebrates exhibits a most typical instance of this form of segmentation.

In Elasmobranchs the first two furrows are formed in a perfectly normal manner, but though I have not observed the actual formation of the next furrow, yet from the later stages, which I have observed, I conclude that it is parallel to one of the first formed furrows; and it is fairly certain that, not till a considerably later period, is a furrow homologous with the horizontal furrow of the Batrachian egg formed. This furrow appears to be represented in the Elasmobranch segmentation by the irregular circumscription of a body of central smaller spheres from a ring of peripheral larger ones (vide Pl. I. figs. 3, 4 and 5).

In the Bird the representative of the horizontal furrow

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[1] *Zeitschrift für Wiss. Zoologie*, Bd. xxiii. 1873.

[2] *Archiv für Micr. Anat.* Bd. ix. 1873.

appears relatively much earlier. It is formed when there are eight segments marked out on the surface of the germinal disc[1]. From Oellacher's[2] account of the segmentation in the fowl[3] it seems certain, as might be anticipated, that this furrow is nearly parallel to the surface of the disc, so that it cuts the earlier formed vertical furrows and causes the segments of the germinal disc to be completely circumscribed below as well as at the surface. In the Elasmobranch egg this is not the case; so that, even after the smaller central segments have become separated from the outer ring of larger ones, none of the segments of the disc are completely circumscribed, and only appear to be so in surface views (vide Pl. I. fig. 6). Segmentation in the Elasmobranch egg differs in the following particulars from that in the Bird's egg:

(1) The equivalent of the horizontal furrow of the Batrachian egg appears much later than in the Bird.

(2) When it has appeared it travels inwards much more slowly.

As a result of these differences, the segments of the germinal disc of the Birds' eggs are much earlier circumscribed on all sides than those of the Elasmobranch egg.

As might be expected, the segmentation of the Elasmobranch egg resembles in many points that of Osseous Fishes (vide Oellacher[4] and Klein[5]). It may be noticed, that with Osseous as with Elasmobranch Fishes, the furrow corresponding with the horizontal furrow of the Amphibian's egg does not appear at as early a period as is normal. The third furrow of an Osseous Fish egg is parallel to one of the first formed pair.

In Oellacher's[6] figures, Pl. XXIII. fig. 19—21, peculiar beadings of the sides of the earlier formed furrows are distinctly shewn. No mention of these is made in the text, but they are unquestionably similar to those I have described in the Elasmobranch furrows. In the case of Elasmobranchs I

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[1] Vide *Elements of Embryology*, p. 23.

[2] *Stricker's Studien*, 1869, Pt. I, Pl. II. fig. 4.

[3] Unfortunately Professor Oellacher gives no account of the surface appearances of the germinal discs of which he describes the sections. It is therefore uncertain to what period his sections belong.

[4] *Zeitschrift für Wiss. Zool.* Bd. XXII. 1872.

[5] *Monthly Microscopical Journal*, March, 1872.

[6] *Loc. cit.*

pointed out that not only were the sides of the furrow beaded, but that there appeared in the protoplasm, close to the furrows, peculiar vacuole-like cavities, precisely similar to the cavities which were the cause of the beadings of the furrows.

The presence of these seems to shew that the molecular cohesion of the protoplasm becomes, as compared with other parts, much diminished in the region where a furrow is about to appear, so that before the protoplasm finally gives way along a particular line to form a furrow, its cohesion is broken at numerous points in this region, and thus a series of vacuole-like spaces is formed.

If this is the true explanation of the formation of these spaces, their presence gives considerable support to the views of Dr Kleinenberg upon the causes of segmentation, so clearly and precisely stated in his monograph upon Hydra; and is opposed to any view which regards the forces which come into play during segmentation as resident in the nucleus.

I have not observed the peculiar threads of protoplasm which Oellacher[1] describes as crossing the commencing segmentation furrows. I have also failed to discover any signs of a concentration of the yolk-spherules, round one or two centres, in the segmentation spheres, similar to that observed by Oellacher in the segmenting eggs of Osseous Fish. The appearances observed by him are probably connected with the behaviour of the nucleus during segmentation, and are related to the curious bodies I have already described.

With reference to the nuclei which Oellacher[2] has described as occurring in the eggs of Osseous Fish during segmentation, there can, I think, be little doubt that they are identical with the peculiar nuclei in the Elasmobranch eggs.

He[3] says:

> In an unsegmented germ there occurred at a certain point in the section......a small aggregation of round bodies. I do not feel satisfied whether these aggregations represent one or more nuclei.
>
> Fig. 29 shews such aggregation; by focusing at its optical section eleven unequally large rounded bodies measuring from 0.004

[1] *Loc. cit.*
[2] *Loc. cit.*
[3] *Loc. cit.* p. 410, 411, &c.

—0.009 *Mm.* may be distinguished. They lay as if in a multi-locular gap in the germ mass, which however they did not quite fill. In each of these bodies there appeared another but far smaller body. These aggregations were distinguished from the germ by an especially beautiful intense violet gold chloride colouration of their elements. The smaller elements contained in the larger were still more intensely coloured than the larger.

He further states that these aggregations equal the segments in number, and that the small bodies within the elements are not always to be seen with the same distinctness.

Oellacher's description as well as his figures of these bodies leaves no doubt in my mind that they are exactly similar bodies to those which I have already spoken of as nuclei, and the characteristic features of which I have shortly mentioned, and shall describe more fully at a later stage. A moderately full description of them is to be found in my preliminary paper[1].

Their division into a series of separate areas each with a deeply-stained body, as well as the staining of the whole of them, exactly corresponds to what I have found. That each is a single nucleus is quite certain, though their knobbed form might occasionally lead to the view of their being divided. This knobbed condition, observed by Oellacher as well as myself, certainly supports the view, that they are in the act of budding off fresh nuclei. Oellacher conceives, that the areas into which these nuclei are divided represent a series of separate bodies—this according to my observations is not the case. Nuclei of the same form have already been described in Nephelis, and are probably not very rare. They pass by insensible gradations into ordinary nuclei with numerous granules.

One marked feature of the segmentation of the Elasmobranch egg is the continuous advance of the process of segmentation into the yolk and the assimilation of this into the germ by the direct formation of fresh segments out of it. Into the significance of this feature I intend to enter fully hereafter; but it is interesting to notice that Oellacher's descriptions point to a similar feature in the segmentation of Osseous Fish. This however consists chiefly in the formation of fresh segments

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[1] *Loc. cit.* p. 415.

from the lower parts of the germinal disc which in Osseous Fish is more distinctly marked off from the food-yolk than in Elasmobranchs.

I conclude my description of the segmentation by a short account of what other investigators have written about its features in these fishes. One of the earliest descriptions of this process was given by Leydig[1]. To his description of the germinal disc, I have already done full justice.

In the first stage of segmentation which he observed 20—30 segments were already visible on the surface. In each of these he recognised a nucleus but no nucleolus.

He rightly states that the segments have no membrane, and describes the yolk-spherules which fill them.

The next investigator is Gerbe[2]. I have unfortunately been unable to refer to this elaborate paper, but I gather from an abstract that M. Gerbe has given a careful description of the external features of segmentation.

Schenk[3] has also made important investigations on the subject. He considers that the ovum is invested with a very delicate membrane. This membrane I have failed to find a trace of, and agree with Leydig[4] in denying its existence. Schenk further found that after impregnation, but before segmentation, the germinal disc divided itself into two layers, an upper and a lower. Between the two a cavity made its appearance which Schenk looks upon as the segmentation cavity. Segmentation commences in the upper of the two layers, but Schenk does not give a precise account of the fate of the lower. I have had no opportunity of investigating the impregnated ovum before the commencement of segmentation, but my observations upon the early stages of this process render it clear that no division of the germinal disc exists subsequently to the commencement of segmentation, and that the cavity discovered by Schenk can have no connection

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[1] *Rochen u. Haie.* It is here mentioned that Coste observed the segmentation in these fishes.

[2] *Recherches sur la segmentation des products adventifs de l'œuf des Plagiostomes et particulièrement des Raies.* Robin, *Journal de l'Anatomie et de la Physiologie*, p. 609, 1872.

[3] *Die Eier von Raja quadrimaculata innerhalb der Eileiter. Sitz. der k. Akad. Wien.* Vol. LXXIII. 1873.

[4] *Loc. cit.* My denial of the existence of this membrane naturally applies only to the egg after impregnation, and to the genera Scyllium and Pristiurus.

whatever with the segmentation cavity. I am indeed inclined to look upon this cavity as an artificial product. I have myself met with somewhat similar appearances, after the completion of segmentation, which were caused by the non-penetration of my hardening reagent beyond a certain point.

Without attempting absolutely to explain the appearances described by Professor Schenk, I think that his observations ought to be repeated, either by himself or some other competent observer.

Several further facts are recorded by Professor Schenk in his interesting paper. He states that immediately after impregnation, the germinal disc presents towards the yolk a strongly convex surface, and that at a later period, but still before the commencement of segmentation, this becomes flattened out. He has further detected amœboid movements in the disc at the same period. As to the changes of the germinal disc during segmentation, his paper contains no facts of importance.

Next in point of time to the paper of Schenk, is my own preliminary account of the development of the Elasmobranch Fishes[1]. In this a large number of the facts here described in full are briefly alluded to.

The last author who has investigated the segmentation in Elasmobranchs, is Dr Alexander Schultz[2]. He merely states that he has observed the segmentation, and confirms Professor Schenk's statements about the amœboid movements of the germinal disc.

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[1] *Loc. cit.*

[2] *Die Embryonal Anlage der Selachier. Vorlaufige Mittheilung, Centralblatt f. Med. Wiss.* No. 33, 1875.

CHAPTER III.

FORMATION OF THE LAYERS.

IN the last chapter the blastoderm was left as a solid lens-shaped mass of cells, thicker at one end than at the other, its uppermost row of cells forming a distinct layer. There very soon appears in it a cavity, the well known segmentation cavity, or cavity of von Baer, which arises as a small space in the midst of the blastoderm, near its non-embryonic end (Pl. III. fig. 1).

This condition of the segmentation cavity, though already[1] described, has nevertheless been met with in one case only. The circumstance of my having so rarely met with this condition is the more striking because I have cut sections of a considerable number of blastoderms in the hope of encountering specimens similar to the one figured, and it can only be explained on one of the two following hypotheses. Either the stage is very transitory, and has therefore escaped my notice except in the one instance; or else the cavity present in this instance is not the true segmentation cavity, but merely some abnormal structure. That this latter explanation is a possible one, appears from the fact that such cavities do at times occur in other parts of the blastoderm. Dr Schultz[2] does not mention having found any stage of this kind.

The position of the cavity in question, and its general appearance, incline me to the view that it is the segmentation cavity[3]. If this is the true view of its nature the fact should be noted that at first its floor is formed by the lower layer cells and not by the yolk, and that its roof is constituted by both the

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[1] *Qy. Journal of Microsc. Science*, Oct. 1874.

[2] *Centr. f. Med. Wiss.* No. 38, 1875.

[3] Professor Bambeke (*Poissons Osseux, Mém. Acad. Belgique* 1875) describes a cavity in the blastoderm of Leuciscus rutilus, which he regards as the true segmentation cavity, but not as identical with the segmentation cavity of Osseous Fishes, usually so called. Its relations are the same as those of my segmentation cavity at this stage. This paper came into my hands at too late a period for me to be able to do more than refer to it in this place.

lower layer cells and the epiblast cells. The relations of the floor undergo considerable modifications in the course of development.

The other features of the blastoderm at this stage are very much those of the previous stage.

The embryonic swelling is very conspicuous. The cells of the blastoderm are still disposed in two layers: an upper one of slightly columnar cells one deep, which constitutes the epiblast, and a lower one consisting of the remaining cells of the blastoderm.

An average cell of the lower layer has a diameter of about $\frac{1}{900}$ inch, but the cells at the periphery of the layer are in some cases considerably larger than the more central ones. All the cells of the blastoderm are still completely filled with yolk spherules. In the yolk outside the peculiar nuclei, before spoken of, are present in considerable numbers. They seem to have been mistaken by Dr Schultz[1] for cells: there can however be no question that they are true nuclei.

In the next stage the relations of the segmentation cavity undergo important modifications.

The cells which form its floor disappear almost completely from that position, and the floor becomes formed by the yolk.

The stage, during which the yolk serves as the floor of the segmentation cavity, extends over a considerable period of time, but during it I have been unable to detect any important change in the constitution of the blastoderm. It no doubt gradually extends over the yolk, but even this growth is not nearly so rapid as in the succeeding stage. Although therefore the stage I proceed to describe is of long continuance, a blastoderm at the beginning of it exhibits, both in its external and in its internal features, no important deviations from one at the end of it.

Viewed from the surface (Pl. VI. fig. A) the blastoderm at this stage appears slightly oval, but the departure from the circular form is not very considerable. The long axis of the oval corresponds with what eventually becomes the long axis of the embryo. From the yolk the blastoderm is

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[1] *Loc. cit.*

still well distinguished by its darker colour; and it is surrounded by a concentric ring of light-coloured yolk, the outer border of which shades insensibly into the normal yolk.

At the embryonic portion of the blastoderm is a slight swelling, clearly shown in Plate VI. fig. A, which can easily be detected in fresh and in hardened embryos. This swelling is to be looked upon as a local exaggeration of a slightly raised rim present around the whole circumference of the blastoderm. The roof of the segmentation cavity (fig. A, *s. c.*) forms a second swelling; and in the fresh embryo this region appears of a darker colour than other parts of the blastoderm.

It is difficult to determine the exact shape of the blastoderm, on account of the traction exercised upon it in opening the egg; and no reliance can be placed on the forms assumed by hardened blastoderms. This remark also applies to the sections of blastoderms of this stage. There can be no doubt that the minor individual variations exhibited by almost every specimen are produced in the course of manipulations while the objects are fresh. These variations may affect even the relative length of a particular region and certainly the curvature of it. The roof of the segmentation cavity is especially apt to be raised into a dome-like form.

The main internal feature of this stage is the disappearance of the layer of cells which, during the first stage, formed the floor of the segmentation cavity. This disappearance is nevertheless not absolute, and it is doubtful whether there is any period in which the floor of the cavity is quite without cells.

Dr Schultz supposes[1] that the entire segmentation cavity is, in the living animal, filled with a number of loose cells. Though it is not in my power absolutely to deny this, the point being one which cannot be satisfactorily investigated in sections, yet no evidence has come under my notice which would lead to the conclusion that more cells are present in the segmentation cavity than are represented on Pl. XIII. fig. 1, of my preliminary paper[2], an illustration which is repeated on Pl. III. fig. 2.

The number of cells on the floor of the cavity differs considerably in different cases, but these cases come under the

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[1] *Loc. cit.*

[2] *Loc. cit.*

category of individual variations, and are not to be looked upon as indications of different states of development.

In many cases especially large cells are to be seen on the floor of the cavity (Pl. III. fig. 2, *b d*). In my preliminary paper[1] the view was expressed that these are probably cells formed around the nuclei of the yolk. This view I am inclined to abandon, and to substitute for it the suggestion made by Dr Schultz, that they are remnants of the larger segmentation cells which were to be seen in the previous stages.

Plate III. figs. 2, 3, 4 (all sections of this stage) show the different appearances presented by the floor of the segmentation cavity. In only one of these sections are there any large number of cells upon the floor; and in no case have cells been observed imbedded in the yolk forming this floor, as described by Dr Schultz[2], but in all cases the cells simply rested upon it.

Passing from the segmentation cavity to the blastoderm itself, the first feature to be noticed is the more decided differentiation of the epiblast. This now forms a distinct layer composed of a single row of columnar cells. These are slightly more columnar in the region of the embryonic swelling than elsewhere, and become less elongated at the edge of the blastoderm. In my specimens this layer was never more than one cell deep, but Dr Schultz[3] states that, in the Elasmobranch embryos investigated by him, the epiblast was composed of more than a single row of cells.

Each epiblast cell is filled with yolk spherules and contains a nucleus. Very frequently the nuclei in the layer are arranged in a regular row (vide Pl. III. fig. 3). In the later blastoderms of this stage there is a tendency in the cells to assume a wedge-like form with their thin ends pointing alternately in opposite directions. This arrangement is, however, by no means strictly adhered to, and the regularity of it is exaggerated in Plate III. fig. 4.

The nuclei of the epiblast cells have the same characters as those of the lower layer cells to be presently described, but their intimate structure can only be successfully studied in

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[1] *Qy. Journal of Micros. Science*, Oct. 1874.

[2] *Loc. cit.* Probably Dr Schultz, here as in other cases, has mistaken nuclei for cells.

[3] *Loc. cit.*

certain exceptionally favourable sections. In most cases the yolk spherules around them render the finer details invisible.

There is at this stage no such obvious continuity as in the succeeding stage between the epiblast and the lower layer cells; and this statement holds good more especially with the best conserved specimens which have been hardened in osmic acid (Plate III. fig. 4). In these it is very easy to see that the epiblast simply thins out at the edge of the blastoderm without exhibiting the slightest tendency to become continuous with the lower layer cells[1].

The lower layer cells form a mass rather than a layer, and constitute the whole of the blastoderm not included in the epiblast. The shape of this mass in a longitudinal section may be gathered from an examination of Plate III. figs. 3 and 4.

It presents an especially thick portion forming the bulk of the embryonic swelling, and frequently contains one or two cavities, which from their constancy I regard as normal and not as artificial products.

In addition to the mass forming the embryonic swelling there is seen in sections another mass of lower layer cells at the opposite extremity of the blastoderm, connected with the former by a bridge of cells, which constitutes the roof of the segmentation cavity. The lower layer cells may thus be divided into three distinct parts:

(1) The embryo swelling.

(2) The thick rim of cells round the edge of the remainder of the blastoderm.

(3) The cells which form the roof of the segmentation cavity.

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[1] Prof. Haeckel (Die Gastrula u. die Eifurchung d. Thiere, *Jenaische Zeitschrift*, Vol. IX.) has unfortunately copied a figure from my preliminary paper (*loc. cit.*) (repeated now), which I had carefully avoided using for the purpose of describing the formation of the layers on account of the epiblast cells in the original having been much altered by the chromic acid, as a result of which the whole section gives a somewhat erroneous impression of the condition of the blastoderm at this stage. I take this opportunity of pointing out that the colouration employed by Professor Haeckel to distinguish the layers in this section is not founded on my statements, but is, on the contrary, in entire opposition to them. From the section as represented by Professor Haeckel it might be gathered that I considered the lower layer cells to be divided into two parts, one derived from the epiblast, while the other constituted the hypoblast. Not only is no such division present at this period, but no part of the lower layer cells, or the mesoblast cells into which they become converted, can in any sense whatever be said to be derived from the epiblast.

These three parts form a continuous whole, but in addition to these there exist the previously mentioned cells, which rest on the floor of the segmentation cavity.

With the exception of these latter, the lower layer is composed of cells having a fairly uniform size, and exhibits no trace of a division into two layers.

The cells are for the most part irregularly polygonal from mutual pressure; and in their shape and arrangement, exhibit a marked contrast to the epiblast cells. A few of the lower layer cells, highly magnified, are represented in Pl. III. fig. 2 *a*. An average cell measures about $\frac{1}{800}$ to $\frac{1}{900}$ of an inch, but some of the larger ones on the floor attain to the $\frac{1}{475}$ of an inch.

Owing to my having had the good fortune to prepare some especially favourable specimens of this stage, it has been possible for me to make accurate observations both upon the nuclei of the cells of the blastoderm, and upon the nuclei of the yolk.

The nuclei of the blastoderm cells, both of the epiblast and lower layer, have a uniform structure. Those of the lower layer cells are about $\frac{1}{1600}$ of an inch in diameter. Roughly speaking each consists of a spherical mass of clear protoplasm refracting more highly than the protoplasm of its cell. The nucleus appears in sections to be divided by deeply stained lines into a number of separate areas, and in each of these a deeply stained granule is placed. In some cases two or more of such granules may be seen in a single area. The whole of the nucleus stains with the colouring reagents more deeply than the protoplasm of the cells; but this is especially the case with the granules and lines.

Though usually spherical the nuclei not infrequently have a somewhat lobate form.

Very similar to these nuclei are the nuclei of the yolk.

One of the most important differences between the two is that of size. The majority of the nuclei present in the yolk are as large or larger than an ordinary blastoderm cell; while many of them reach a size very much greater than this. The examples I have measured varied from $\frac{1}{500}$ to $\frac{1}{250}$ of an inch in diameter.

Though they are divided, like the nuclei of the blastoderm, with more or less distinctness into separate areas by a network of lines, their greater size frequently causes them to present an aspect somewhat different from the nuclei of the blastoderm. They are moreover much less regular in outline than these, and very many of them have lobate projections (Pl. III. figs. 2*a* and 2*c* and 3), which vary from simple knobs to projections of such a size as to cause the nucleus to present an appearance of commencing constriction into halves. When there are several such projections the nucleus acquires a peculiar knobbed figure. With bodies of this form it becomes in many cases a matter of great difficulty to decide whether or no a particular series of knobs, which appear separate in one plane, are united in a lower plane, whether, in fact, there is present a single knobbed nucleus or a number of nuclei in close apposition. A nucleus in this condition is represented in Pl. III. fig. 2 *b*.

The existence of a protoplasmic network in the yolk has already been mentioned. This in favourable cases may be observed to be in special connection with the nuclei just described. Its meshes are finer in the vicinity of the nuclei, and its fibres in some cases almost appear to start from them (Pl. V. fig. 12). For reasons which I am unable to explain the nuclei of the yolk and the surrounding meshwork present appearances which differ greatly according to the reagent employed. In most specimens hardened in osmic acid the protoplasm of the nuclei is apparently prolonged in the surrounding meshwork (Pl. V. fig. 12). In other specimens hardened in osmic acid (Pl. V. fig. 11), and in all hardened in chromic acid (Pl. III. fig. 2 *a* and 2 *c*), the appearances are far clearer than in the previous case, and the protoplasmic meshwork merely surrounds the nuclei, without showing any signs of becoming continuous with them.

There is also around each nucleus a narrow space in which the spherules of the yolk are either much smaller than elsewhere or completely absent, vide Pl. III. fig. 2 *b*.

It has not been possible for me to satisfy myself as to the exact meaning of the lines dividing these nuclei into a number of distinct areas. My observations leave the question open as to whether they are to be looked upon as lines of division, or as protoplasmic lines such as have been described in nuclei by Flemming[1], Hertwig[2] and Van Beneden[3]. The latter view appears to me to be the more probable one.

Such are the chief structural features presented by these nuclei, which are present during the whole of the earlier periods of development and retain throughout the same appearance. There can be little doubt that their knobbed condition implies that they are undergoing a rapid division. The arguments for this view I have already insisted on, and, in spite of the observations of Dr Kleinenberg showing that similar nuclei of Nephelis do not undergo division, the case for their doing so in the Elasmobranch eggs is to my mind a very strong one.

During this stage the distribution of these nuclei in the yolk becomes somewhat altered from that in the earlier stages. Although the nuclei are still scattered generally throughout the finer yolk-matter around the blastoderm, yet they are especially aggregated at one or two points. In the first place a special collection of them may be noticed immediately below the floor of the segmentation cavity. They here form a distinct row or even layer. If the presence of this layer is coupled with the fact that at this period cells are beginning to appear on the floor of the segmentation cavity, a strong argument is obtained for the supposition that around these nuclei cells are being produced, which pass into the blastoderm to form the floor. Of the actual formation of cells at *this* period I have not been able to obtain any satisfactory example, so that it remains a matter of deduction rather than of direct observation.

Another special aggregation of nuclei is generally present at the periphery of the blastoderm, and the same amount of doubt hangs over the fate of these as over that of the previously mentioned nuclei.

The next stage is the most important in the whole history of the formation of the layers. Not only does it serve to show, that the process by which the layers are formed in Elasmo-

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[1] Entwicklungsgeschichte der Najaden, *Sitz. d. k. Akad. Wien*, 1875.

[2] *Morphologische Jahrbuch*, Vol. I. Heft 3.

[3] Développement des Mammifères, *Bul. de l'Acad. de Belgique*, XL. No. 12, 1875.

branchs can easily be derived from a simple gastrula type like that of Amphioxus, but it also serves as the key by which other meroblastic types of development may be explained. At the very commencement of this stage the embryonic swelling becomes more conspicuously visible than it was. It now projects above the level of the yolk in the form of a rim. At one point, which eventually forms the termination of the axis of the embryo, this projection is at its greatest; while on either side of this it gradually diminishes and finally vanishes. This projection I propose calling, as in my preliminary paper[1], the embryonic rim.

The segmentation cavity can still be seen from the surface, and a marked increase in the size of the blastoderm may be noticed. During the stage last described, the growth was but very slight; hence the rather sudden and rapid growth which now takes place becomes striking.

Longitudinal sections at this stage, as at the earlier stages, are the most instructive. Such a section on the same scale as Pl. III. fig. 4, is represented in Pl. III. fig. 5. It passes parallel to the long axis of the embryo, through the point of greatest development of the embryonic rim.

The three fresh features of the most striking kind are (1) the complete envelopment of the segmentation cavity within the lower layer cells, (2) the formation of the embryonic rim, (3) the increase in distance between the posterior end of the blastoderm and the segmentation cavity. The segmentation cavity has by no means relatively increased in size. The roof has precisely its earlier constitution, being composed of an internal lining of lower layer cells and an external one of epiblast. The thin lining of lower layer cells is, in the course of mounting the sections, very apt to fall off; but I am absolutely satisfied that it is never absent.

The floor of the cavity has undergone an important change, being now formed by a layer of cells instead of by the yolk. A precisely similar but more partial change in the constitution of the floor takes place in Osseous Fishes[2].

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[1] *Qy. Journal Microsc. Science*, Oct. 1874.

[2] Götte, Der Keim d. Forelleneies, *Arch. f. Mikr. Anat.* Vol. IX.; Haeckel, Die Gastrula u. die Eifurchung d. Thiere, *Jenaische Zeitschrift*, Bd. IX.

The mode in which the floor is formed is a question of some importance. The nuclei, which during the last stage formed a row beneath it, probably, as previously pointed out, take some share in its formation. An additional argument to those already brought forward in favour of this view may be derived from the fact that during this stage such a row of nuclei is no longer present.

This argument may be stated as follows:

Before the floor of cells for the segmentation cavity is formed a number of nuclei are present in a suitable situation to supply the cells for the floor; as soon as the floor of cells makes its appearance these nuclei are no longer to be seen. From this it may be concluded that their disappearance arises from their having become the nuclei of the cells which form the floor.

It appears to me most probable that there is a growth inwards from the whole peripheral wall of the cavity, and that this ingrowth, as well as the cells derived from the yolk, assist in forming the floor of the cavity. In Osseous Fish there appears to be no doubt that the floor is largely formed by an ingrowth of this kind.

A great increase is observable in the distance between the posterior end of the segmentation cavity and the edge of the blastoderm. This is due to the rapid growth of the latter combined with the stationary condition of the former. The growth of the blastoderm at this period is not uniform, but is more rapid in the non-embryonic than in the embryonic parts.

The main features of the epiblast remain the same as during the last stages. It is still composed of a very distinct layer one cell deep. Over the segmentation cavity, and over the whole embryonic end of the blastoderm, the cells are very thin, columnar, and, roughly speaking, wedge-shaped with the thin ends pointing alternately in different directions. For this reason, the nuclei form two rows; but both the rows are situated near the upper surface of the layer (vide Pl. III. fig. 5). Towards the posterior end of the blastoderm the cells are flatter and broader; and the layer terminates at the non-embryonic end of the blastoderm without exhibiting the slightest tendency to become continuous with the lower layer cells. At the embryonic end of the blastoderm the relations of the epiblast and lower layer cells are very different. At this part, throughout the whole extent of the embryonic rim, the epiblast is reflected and becomes continuous with the lower layer cells.

The lower layer cells form, for the most part, a uniform stratum in which no distinction into mesoblast and hypoblast is to be seen.

Both the lower layer cells and the epiblast cells are still filled with yolk spherules.

The structures at the embryonic rim, and the changes which are there taking place, unquestionably form the chief features of interest at this stage.

The general relations of these parts are very fairly shown in Pl. III. fig. 5, which represents a section passing through the median line of the embryonic region. They are however more accurately represented in Pl. IV. fig. 5 *a*, taken from the same embryo, but in a lateral part of the embryonic rim; or in Pl. IV. fig. 6, from a slightly older embryo. In all of these figures the epiblast cells are reflected at the edge of the embryonic rim, and become perfectly continuous with the hypoblast cells. A few of the cells, immediately beyond the line of this reflection, precisely resemble in character the typical epiblast cells; but the remainder exhibit a gradual transition into typical lower layer cells. Adjoining these transitional cells, or partly enclosed in the corner formed between them and the epiblast, are a few unaltered lower layer cells (*m*), which at this stage are not distinctly separated from the transitional cells. The transitional cells form the commencement of the hypoblast (*hy*); and the cells (*m*) between them and the epiblast form the commencement of the mesoblast. The gradual conversion of lower layer cells into columnar hypoblast cells, is a very clear and observable phenomenon in the best specimens. Where the embryonic rim projects most, a larger number of cells have assumed a columnar form. Where it projects less clearly, a smaller number have done so. But in all cases there may be observed a series of gradations between the columnar cells and the typical rounded lower layer cells[1].

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[1] When writing my earlier paper I did not feel so confident about the mode of formation of the hypoblast as I now do, and even doubted the possibility of determining it from sections. The facts now brought forward are I hope sufficient to remove all scepticism on this point.

In the last described embryo, although the embryonic rim had attained to a considerable development, no trace of the medullary groove had made its appearance. In an embryo in the next stage of which I propose describing sections, this structure has become visible.

A surface view of a blastoderm of this age, with the embryo, is represented on Pl. VI. fig. B; and I shall, for the sake of convenience, in future speak of embryos of this age as belonging to period B.

The blastoderm is nearly circular. The embryonic rim is represented by a darker shading at the edge. At one point in this rim may be seen the embryo, consisting of a somewhat raised area with an axial groove (*m g*). The head end of the embryo is that which points towards the centre of the blastoderm, and its free peripheral extremity is at the edge of the blastoderm.

A longitudinal section of an embryo of the same age as the one figured[1] is represented on Pl. IV. fig. 7. The general growth has been very considerable, though as before explained, it is mainly confined to that part of the blastoderm where the embryonic rim is absent.

A fresh feature of great importance is the complete disappearance of the segmentation cavity, the place which was previously occupied by it being now filled up by an irregular network of cells. There can be little question that the obliteration of the segmentation cavity is in part due to the entrance into the blastoderm of fresh cells formed around the nuclei of the yolk. The formation of these is now taking place with great rapidity and can be very easily followed.

Since the segmentation cavity ceases to play any further part in the history of the blastoderm, it will be well shortly to review the main points in its history.

Its earliest appearance is involved in some obscurity, though it probably arises as a simple cavity in the midst of the lower layer cells (Pl. III. fig. 1). In its second phase the floor ceases to be formed of lower layer cells, and the place of these is taken by the yolk, on which however a few scattered cells

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[1] Owing to the small size of the plates this section has been drawn on a considerably smaller scale than that represented in fig. 5.

still remain (Pl. III. figs. 2, 3, 4). During the third period of its history, a distinct cellular floor is again formed for it, so that it comes a second time into the same relations with the blastoderm as at its earliest appearance. The floor of cells which it receives is in part due to a growth inwards from the periphery of the blastoderm, and in part to the formation of fresh cells from the yolk. Coincidently with the commencing differentiation of hypoblast and mesoblast the segmentation cavity grows smaller and vanishes.

One of the most important features of the segmentation cavity in the Elasmobranchs which I have studied, is the fact that throughout its whole existence its roof is formed of *lower layer cells.* There is not the smallest question that the segmentation cavity of these fishes is the homologue of that of Amphioxus, Batrachians, etc., yet in the case of all of these animals, the roof of the segmentation cavity is formed of epiblast only. How comes it then to be formed of lower layer cells in Elasmobranchii ?

To this question an answer was attempted in my paper, "Upon the Early Stages of the Development of Vertebrates[1]." It was there pointed out, that as the food material in the ovum increases, the bulk of the lower layer cells necessarily also increases; since these, as far as the blastoderm is concerned, are the chief recipients of food material. This causes the lower layer cells to encroach upon the segmentation cavity, and to close it in not only on the sides, but also above; from the same cause it results that the lower layer cells assume, from the first, a position around the spot where the future alimentary cavity will be formed, and that this cavity becomes formed by a simple split in the midst of the lower layer cells, and not by an involution.

All the most recent observations[2] on Osseous Fishes tend to show that in them, the roof of the segmentation cavity is formed alone of epiblast; but on account of the great difficulty which is experienced in distinguishing the layers in the blastoderms of these animals, I still hesitate to accept as conclusive the testimony on this point.

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[1] *Quart. Journ. of Microscop. Science*, July, 1875.

[2] Oellacher, *Zeit. f. Wiss. Zoologie*, Bd. XXIII. Götte, *Archiv f. Mikr. Anat.* Vol. IX. Haeckel, *loc. cit.*

In the formation a second time of a cellular floor for the segmentation cavity in the third stage, the Elasmobranch embryo seems to resemble that of the Osseous Fish[1]. Upon this feature great stress is laid both by Dr Götte[2] and Prof. Haeckel[3]: but I am unable to agree with the interpretation of it offered by them. Both Dr Götte and Prof. Haeckel regard the formation of this floor as part of an involution to which the lower layer cells owe their origin, and consider the involution an equivalent to the alimentary involution of Batrachians, Amphioxus, &c. To this question I hope to return, but it may be pointed out that my observations prove that this view can only be true in a very modified sense; since the invagination by which hypoblast and alimentary canal are formed in Amphioxus is represented in Elasmobranchs by a structure quite separate from the ingrowth of cells to form the floor of the segmentation cavity.

The eventual *obliteration* of the segmentation cavity by cells derived from the yolk is to be regarded as an inherited remnant of the involution by which this obliteration was primitively effected. The passage upwards of cells from the yolk, may possibly be a real survival of the tendency of the hypoblast cells to grow inwards during the process of involution.

The last feature of the segmentation cavity which deserves notice is its excentric position. It is from the first situated in much closer proximity to the non-embryonic than to the embryonic end of the blastoderm. This peculiarity in position is also characteristic of the segmentation cavity of Osseous Fishes, as is shown by the concordant observations of Oellacher[4] and Götte[5]. Its meaning becomes at once intelligible by referring to the diagrams in my paper[6] on the Early Stages in the Development of Vertebrates. It in fact arises from the asymmetrical character of the primitive alimentary involution in all anamniotic vertebrates with the exception of Amphioxus.

Leaving the segmentation cavity I pass on to the other features of my sections.

There is still to be seen a considerable aggregation of cells at the non-embryonic end of the blastoderm. The position of this, and its relations with the portion of the blastoderm which

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[1] This floor appears in most Osseous Fish to be only partially formed. Vide Götte, *loc. cit.*

[2] *Loc. cit.* [3] *Loc. cit.* [4] *Loc. cit.* [5] *Loc. cit.* [6] *Loc. cit.*

at an earlier period contained the segmentation cavity, indicate that the growth of the blastoderm is not confined to its edge, but that it proceeds at all points causing the peripheral parts to glide over the yolk.

The main features of the cells of this blastoderm are the same as they were in the one last described. In the non-embryonic region the epiblast has thinned out, and is composed of a single row of cells, which, in the succeeding stages, become much flattened.

The lower layer cells over the greater part of their extent, have not undergone any histological changes of importance. Amongst them may frequently be seen a few exceptionally large cells, which without doubt have been derived directly from the yolk.

The embryonic rim is now a far more considerable structure than it was. Vide Pl. IV. fig. 7. Its elongation is mainly effected by the continuous conversion of rounded lower layer cells into columnar hypoblast cells at its central or anterior extremity.

This conversion of the lower layer cells into hypoblast cells is still easy to follow, and in every section cells intermediate between the two are to be seen. The nature of the changes which are taking place requires for its elucidation transverse as well as longitudinal sections. Transverse sections of a slightly older embryo than B are represented on Pl. IV. fig. 8 *a*, 8 *b*, and 8 *c*.

Of these sections *a* is the most peripheral or posterior, and *c* the most central or anterior. By a combination of transverse and longitudinal sections, and by an inspection of a surface view, it is rendered clear that, though the embryonic rim is a far more considerable structure in the region of the embryo than elsewhere (compare fig. 6 and fig. 7 and 7 *a*), yet that this gain in size is not produced by an outgrowth of the embryo beyond the rest of the germ, but by the conversion of the lower layer cells into hypoblast having been carried far further towards the centre of the germ in the axial line than in the lateral regions of the rim.

The most anterior of the series of transverse sections (Pl. IV. fig. 8 *c*) I have represented, is especially instructive with reference to this point. Though the embryonic rim is cut through at the sides of the section, yet in these parts the rim consists of hardly more than a continuity between epiblast and lower layer cells, and the lower layer cells show no trace of a division into mesoblast and hypoblast. In the axis of the embryo, however, the columnar hypoblast is quite distinct; and on it a small cap of mesoblast is seen on each side of the medullary groove. Had the embryonic rim resulted from a projecting growth of the blastoderm, such a condition could not have existed. It might have been possible to find the hypoblast formed at the sides of the section and not at the centre; but the reverse, as in these sections, could not have occurred. Indeed it is scarcely necessary to have recourse to sections to prove that the growth of the embryonic rim is towards the centre of the blastoderm. The inspection of a surface view of a blastoderm at this period demonstrates it beyond a doubt (Pl. VI. fig. B). The embryo, close to which the embryonic rim is alone largely developed, does not project outwards beyond the edge of the germ, but inwards towards its centre.

The space between the embryonic rim and the yolk (Pl. IV. fig. 7 *al.*) is the alimentary cavity. The roof of this is therefore primitively formed of hypoblast and the floor of yolk. The external opening of this space at the edge of the blastoderm is the exact morphological homologue of the anus of Rusconi, or blastopore of Amphioxus, the Amphibians, &c. The importance of the mode of growth in the embryonic rim depends upon the homology of the cavity between it and the yolk, with the alimentary cavity of Amphioxus and Amphibians. Since this homology exists, the direction of the growth of this cavity ought to be, as it in fact is, the same as in Amphioxus, etc., viz. towards the centre of germ and original position of the segmentation cavity. Thus though a true invagination is not present as in the other cases, yet this is represented in Elasmobranchs by the continuous conversion of lower layer cells into hypoblast along a line leading towards the centre of the blastoderm.

In the parts of the rim adjoining the embryo, the lower layer cells, on becoming continuous with the epiblast cells, assume a columnar form. At the sides of the rim this is not strictly the case, and the lower layer cells retain their rounded form, though quite continuous with the epiblast cells. One curious feature of the layer of epiblast in these lateral parts of the rim is the great thickness it acquires before being reflected and becoming continuous with the hypoblast (Pl. IV. fig. 8*c*). In the vicinity of the point of reflection there is often a rather large formation of cells around the nuclei of the yolk. The cells formed here no doubt pass into the blastoderm, and become converted into columnar hypoblast cells. In some cases the formation of these cells is very rapid, and they produce quite a projection on the under side of the hypoblast. Such a case is represented in Pl. IV. fig. 8 *b*, *n. al.* The cells constituting this mass eventually become converted into the lateral and ventral walls of the alimentary canal.

The formation of the mesoblast has progressed rapidly. While many of the lower layer cells become columnar and form the hypoblast, others, between these and the epiblast, remain spherical. The latter do not at once become separated as a layer distinct from the hypoblast, and, at first, are only to be distinguished from them through their different character, vide Plate IV. figs. 6 and 7. They nevertheless constitute the commencing mesoblast.

Thus much of the mode of formation of the mesoblast can be easily made out in longitudinal sections, but transverse sections throw still further light upon it.

From these it may at once be seen that the mesoblast is not formed in one continuous sheet, but as two lateral masses, one on each side of the axial line of the embryo[1]. In my preliminary account[2] it was stated that this was a condition of the mesoblast at a very early period, and that it was probably its condition from the beginning. Sections are now in my possession which satisfy me that, from the very first, the mesoblast arises as two distinct lateral masses, one on each side of the axial line.

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[1] Professor Lieberkühn (*Gesellschaft zu Marburg*, Jan. 1876) finds in Mammalia a bilateral arrangement of the mesoblast, which he compares with that described by me in Elasmobranchs. In Mammalia, however, he finds the two masses of mesoblast connected by a very thin layer of cells, and is apparently of opinion that a similar thin layer exists in Elasmobranchs though overlooked by me. I can definitely state that, whatever may be the condition of the mesoblast in Mammalia, in Elasmobranchs at any rate no such layer exists.

[2] *Loc. cit.*

In the embryo from which the sections Pl. IV. fig. 8 *a*, 8 *b*, 8 *c* were taken, the mesoblast had, in most parts, not yet become separated from the hypoblast. It still formed with this a continuous layer, though the mesoblast cells were distinguishable by their shape from the hypoblast. In only one section (*b*) was any part of the mesoblast quite separated from the hypoblast.

In the hindermost part of the embryo the mesoblast is at its maximum, and forms, on each side, a continuous sheet extending from the median line to the periphery (fig. 8 *a*). The rounder form of the mesoblast cells renders the line of junction between the layer constituted by them and the hypoblast fairly distinct; but towards the periphery, where the hypoblast cells have the same rounded form as the mesoblast, the fusion between the two layers is nearly complete.

In an anterior section the mesoblast is only present as a cap on both sides of the medullary groove, and as a mass of cells at the periphery of the section (fig. 8 *b*); but no continuous layer of it is present. In the foremost of the three sections (fig. 8 *c*) the mesoblast can scarcely be said to have become in any way separated from the hypoblast except at the summit of the medullary folds (*m*).

From these and similar sections it may be certainly concluded, that the mesoblast becomes first separated from the hypoblast as a distinct layer in the posterior region of the embryo, and only at a later period in the region of the head.

In an embryo but slightly more developed than B, the formation of the layer is quite completed in the region of the embryo. To this embryo I now pass on.

In the non-embryonic parts of the blastoderm no fresh features of interest have appeared. It still consists of two layers. The epiblast is composed of flattened cells, and the lower layer of a network of more rounded cells, elongated in a lateral direction. The growth of the blastoderm has continued to be very rapid.

In the region of the embryo (Pl. IV. fig. 9) more important changes have occurred. The epiblast still remains as a single row of columnar cells. The hypoblast is no longer fused with the mesoblast, and forms a distinct dorsal wall for the alimentary cavity. Though along the axis of the embryo the hypoblast is composed of a single row of columnar cells, yet in the lateral part of the embryo its cells are less columnar and are one or two deep.

Owing to the manner in which the mesoblast became split off from the hypoblast, a continuity is maintained between the hypoblast and the lower layer cells of the blastoderm (Pl. IV. fig. 9), while the two plates of mesoblast are isolated and disconnected from any other masses of cells.

The alimentary cavity is best studied in transverse sections. (*Vide* Pl. V. fig. 10 *a*, 10 *b* and 10*c*, three sections from the same embryo.) It is closed in above and at the sides by the hypoblast, and below by the yolk. In its anterior part a floor is commencing to be formed by a growth of cells from the walls of the two sides. The cells for this growth are formed around the nuclei of the yolk; a feature which recalls the fact that in Amphibians the ventral wall of the alimentary cavity is similarly formed in part from the so-called yolk cells.

We left the mesoblast as two masses not completely separated from the hypoblast. During this stage the separation between the two becomes complete, and there are formed two great lateral plates of mesoblast cells, one on each side of the medullary groove. Each of these corresponds to a united vertebral and lateral plate of the higher Vertebrates. The plates are thickest in the middle and posterior regions (Pl. V. fig. 10 *a* and 10 *b*), but thin out and almost vanish in the region of the head. The longitudinal section of this stage represented in Pl. V. fig. 9, passes through one of the lateral masses of mesoblast cells, and shows very distinctly its complete independence of all the other cells in the blastoderm.

From what has been stated with reference to the development of the mesoblast, it is clear that in Elasmobranchs this layer is derived from the same mass of cells as the hypoblast, and receives none of its elements from the epiblast. In connection with its development, as two independent lateral masses, I may observe, as I have previously done[1], that in this respect it bears a close resemblance to mesoblast in Euaxes, as de-

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[1] *Quart. Journ. of Microsc. Science*, Oct., 1874.

scribed by Kowalevsky[1]. This resemblance is of some interest, as bearing on a probable Annelid origin of Vertebrata. Kowalevsky has also shown[2] that the mesoblast in Ascidians is similarly formed as two independent masses, one on each side of the middle line.

It ought, however, to be pointed out that a similar bilateral origin of the mesoblast had been recently met with in Lymnœus by Carl Rabl[3]. A fact which somewhat diminishes the genealogical value of this feature in the mesoblast in Elasmobranchs.

During the course of this stage the spherules of food-yolk immediately beneath the embryo are used up very rapidly. As a result of this the protoplasmic network, so often spoken of, comes very plainly into view. Considerable areas may sometimes be seen without any yolk spherule whatever.

On Pl. IV. fig. 7 *a*, and Pl. V. 11 and 12, I have attempted to reproduce the various appearances presented by this network: and these figures give a better idea of it than any description. My observations tend to show that it extends through the whole yolk, and serves to hold it together. It has not been possible for me to satisfy myself that it had any definite limits, but on the other hand, in many parts all my efforts to demonstrate its presence have failed. When the yolk spherules are very thickly packed, it is difficult to make out for certain whether it is present or absent, and I have not succeeded in removing the yolk spherules from the network in cases of this kind. In medium-sized ovarian eggs this network is very easily seen, and extends through the whole yolk. Part of such an egg is shown in Pl. V. fig. 14. In full-sized ovarian eggs, according to Schultz[4], it forms, as was mentioned in the first chapter, radiating striæ, extending from the centre to the periphery of the egg. When examined with the highest powers, the lines of this network appear to be composed of immeasurably small granules arranged in a linear direction. These granules are more distinct in chromic acid specimens than in

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[1] Embryologische Studien an Würmen u. Arthropoden. *Mémoires d. l'Acad. S. Pétersbourg.* Vol. XIV. 1873.

[2] *Archiv für Mikr. Anat.* Vol. VII.

[3] *Jenaische Zeitschrift.* Vol. IX. 1875. A bilateral development of mesoblast, according to Professor Haeckel (*loc. cit.*), occurs in some Osseous Fish. Hensen, *Zeit. für Anat. u. Entw.* Vol. I., has recently described the mesoblast in Mammalia as consisting of independent lateral masses.

[4] *Archiv für Mikr. Anat.* Vol. XI.

those hardened in osmic acid, but are to be seen in both. There can be little doubt that these granules are imbedded in a thread or thin layer of protoplasm.

I have already (p. 39) touched upon the relation of this network to the nuclei of the yolk[1].

During the stages which have just been described specially favourable views are frequently to be obtained of the formation of cells in the yolk and their entrance into the blastoderm. Two representations of these are given, in Pl. IV. fig. 7 *a*, and Pl. V. fig. 13. In both of these distinctly circumscribed cells are to be seen in the yolk (*c*), and in all cases are situated near to the typical nuclei of the yolk. The cells in the yolk have such a relation to the surrounding parts, that it is quite certain that their presence is not due to artificial manipulation, and in some cases it is even difficult to decide whether or no a cell area is circumscribed round a nucleus (Pl. V. fig. 13). Although it would be possible for cells in the living state to pass from the blastoderm into the yolk, yet the view that they have done so in the cases under consideration has not much to recommend it, if the following facts be taken into consideration. (1) That the cells in the yolk are frequently larger than those in the blastoderm. (2) That there are present a very large number of nuclei in the yolk which precisely resemble the nuclei of the cells under discussion. (3) That in some cases (Pl. V. fig. 13) cells are seen indistinctly circumscribed as if in the act of being formed.

Between the blastoderm and the yolk may frequently be seen a membrane-like structure, which becomes stained with hæmatoxylin, osmic acid etc. It appears to be a layer of coagulated albumen and not a distinct membrane.

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[1] A protoplasmic network resembling in its essential features the one just described has been noticed by many observers in other ova. Fol has figured and described a network or sponge-like arrangement of the protoplasm in the eggs of Geryonia. (*Jenaische Zeitschrift*, vol. VII.) Metschnikoff (*Zeitschrift f. Wiss. Zoologie*, 1874) has demonstrated its presence in the ova of many Siphonophoriæ and Medusæ. Flemming (*Entwicklungsgeschichte der Najaden, Sitz. der k. Akad. Wien*, 1875) has found it in the ovarian ova of fresh-water mussels (Anodonta and Unio), but regards it as due to the action of reagents, since he fails to find it in the fresh condition. Amongst vertebrates it has been carefully described by Eimer (*Archiv für Mikr. Anat.*, vol. VIII.) in the ovarian ova of Reptiles. Eimer moreover finds that it is continuous with prolongations from cells of the epithelium of the follicle in which the ovum is contained. According to him remnants of this network are to be met with in the ripe ovum, but are no longer present in the ovum when taken from the oviduct.

SUMMARY.

At the close of segmentation, the blastoderm forms a somewhat lens-shaped disc, thicker at one end than at the other; the thicker end being termed the embryonic end.

It is divided into two layers—an upper one, the epiblast, formed by a single row of columnar cells; and a lower one, consisting of the remaining cells of the blastoderm.

A cavity next appears in the lower layer cells, near the non-embryonic end of the blastoderm, but the cells soon disappear from the floor of this cavity which then comes to be constituted by yolk alone.

The epiblast in the next stage is reflected for a small arc at the embryonic end of the blastoderm, and becomes continuous with the lower layer cells; at the same time some of the lower layer cells of the embryonic end of the blastoderm assume a columnar form, and constitute the commencing hypoblast. The portion of the blastoderm, where epiblast and hypoblast are continuous, forms a projecting structure which I have called the embryonic rim. This rim increases rapidly by growing inwards more and more towards the centre of the blastoderm, through the continuous conversion of lower layer cells into columnar hypoblast.

While the embryonic rim is being formed, the segmentation cavity undergoes important changes. In the first place, it receives a floor of lower layer cells, partly from an ingrowth from the two sides, and partly from the formation of cells around the nuclei of the yolk.

Shortly after the floor of cells has appeared, the whole segmentation cavity becomes obliterated.

When the embryonic rim has attained to some importance, the position of the embryo becomes marked out by the appearance of the medullary groove at its most projecting part. The embryo extends from the edge of the blastoderm inwards towards the centre.

At about the time of the formation of the medullary groove, the mesoblast becomes definitely constituted. It arises as two independent plates, one on each side of the medullary groove, and is entirely derived from lower layer cells.

The two plates of mesoblast are at first unconnected with any other cells of the blastoderm, and, on their formation, the hypoblast remains in connection with all the remaining lower layer cells. Between the embryonic rim and the yolk is a cavity,—the primitive alimentary cavity. Its roof is formed of hypoblast, and its floor of yolk. Its external opening is homologous with the anus of Rusconi, of Amphioxus and the Amphibians. The ventral wall of the alimentary cavity is eventually derived from cells formed in the yolk around the nuclei which are there present.

Since the important researches of Gegenbaur[1] upon the meroblastic vertebrate eggs, it has been generally admitted that the ovum of every vertebrate, however complicated may be its apparent constitution, is nevertheless to be regarded as a simple cell. This view is, indeed, opposed by His[2] and to a very modified extent by Waldeyer[3], and has recently been attacked from an entirely new standpoint by Götte[4]; but, to my mind, the objections of these authors do not upset the well founded conclusions of previous observations.

As soon as the fact is recognised that both meroblastic and holoblastic eggs have the same fundamental constitution, the admission follows, naturally, though not necessarily, that the eggs belonging to these two classes differ solely in degree, not only as regards their constitution, but also as regards the manner in which they become respectively converted into the embryo. As might have been anticipated, this view has gained a wide acceptance.

Amongst the observations, which have given a strong objective support to this view, may be mentioned those of Professor Lankester upon the development of Cephalopoda[5], and of Dr Götte[6] upon the development of the Hen's egg. In Loligo Professor Lankester showed that there appeared, in

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[1] Wirbelthiereier mit partieller Dottertheilung. *Müller's Arch.* 1861.

[2] *Erste Anlage des Wirbelthierleibes.*

[3] *Eierstock u. Ei.*

[4] *Entwicklungsgeschichte der Unke.* The important researches of Götte on the development of the ovum, though meriting the most careful attention, do not admit of discussion in this place.

[5] *Annals and Magaz. of Natural History*, Vol. XI. 1873, p. 81.

[6] *Archiv f. Mikr. Anat.* Vol. x.

the part of the egg usually considered as food-yolk, a number of bodies, which eventually developed a nucleus and became cells, and that these cells entered into the blastoderm. These observations demonstrate that in the eggs of Loligo the so-called food-yolk is merely equivalent to a part of the egg which in other cases undergoes segmentation.

The observations of Dr Götte have a similar bearing. He made out that in the eggs of the Hen no sharp line is to be found separating the germinal disc from the yolk, and that, independently of the normal segmentation, a number of cells are derived from that part of the egg hitherto regarded as exclusively food-yolk. This view of the nature of the food-yolk was also advanced in my preliminary account of the development of Elasmobranchs[1], and it is now my intention to put forward the positive evidence in favour of this view, which is supplied from a knowledge of the phenomena of the development of the Elasmobranch ovum; and then to discuss how far the facts of the growth of the blastoderm in Elasmobranchs accord with the view that their large food-yolk is exactly equivalent to part of the ovum, which in Amphibians undergoes segmentation, rather than some fresh addition, which has no equivalent in the Amphibian or other holoblastic ovum.

Taking for granted that the ripe ovum is a single cell, the question arises whether in the case of meroblastic ova the cell is not constituted of two parts completely separated from one another.

Is the meroblastic ovum, before or after impregnation, composed of a germinal disc in which *all* the protoplasm of the cell is aggregated, and of a food-yolk in which *no* protoplasm is present? or is the protoplasm present *throughout*, being simply *more concentrated* at the germinal pole than elsewhere? If the former alternative is accepted, we must suppose that the mass of food-yolk is a something added which is not present in holoblastic ova. If the latter alternative is accepted, it may then be maintained that holoblastic and meroblastic ova are constituted in the same way and differ only in the proportions of their constituents.

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[1] *Quart. Journ. of Micr. Science*, Oct. 1874.

My own observations in conjunction with the specially interesting observations of Dr Schultz[1] justify the view which regards the protoplasm as present throughout the whole ovum, and not confined to the germinal disc. Our observations show that a fine protoplasmic network, with ramifications extending throughout the whole yolk, is present both before and after impregnation.

The presence of this network is, in itself, only sufficient to prove that the yolk *may* be equivalent to part of a holoblastic ovum; to demonstrate that it is so requires something more, and this link in the chain of evidence is supplied by the nuclei of the yolk, which have been so often referred to.

These nuclei arise independently in the yolk, and become the nuclei of cells which enter the germ and the bodies of which are derived from the protoplasm of the yolk. Not only so, but the cells formed around these nuclei play the same part in the development of Elasmobranchs as do the largest so-called yolk cells in the development of Amphibians. Like the homologous cells in Amphibians, they mainly serve to form the ventral wall of the alimentary canal and the blood-corpuscles. The identity in the fate of the so-called yolk cells of Amphibians with the cells derived from the yolk in Elasmobranchs, must be considered as a proof of the homology of the yolk cells in the first case with the yolk in the second; the difference between the yolk in the two cases arising from the fact that in the Elasmobranch ovum the yolk spherules bear a larger proportion to the protoplasm than they do in the Amphibian ovum. As I have suggested elsewhere[2], the segmentation or non-segmentation of a particular part of the ovum depends solely upon the proportion borne by the protoplasm to the yolk particles; so that, when the latter exceed the former in a certain fixed proportion, segmentation is no longer possible; and, as this limit is approached, segmentation becomes slower, and the resulting segments larger and larger.

The question how far the facts in the developmental history of the various vertebrate blastoderms accord with the view of the nature of the yolk just propounded, is one of considerable

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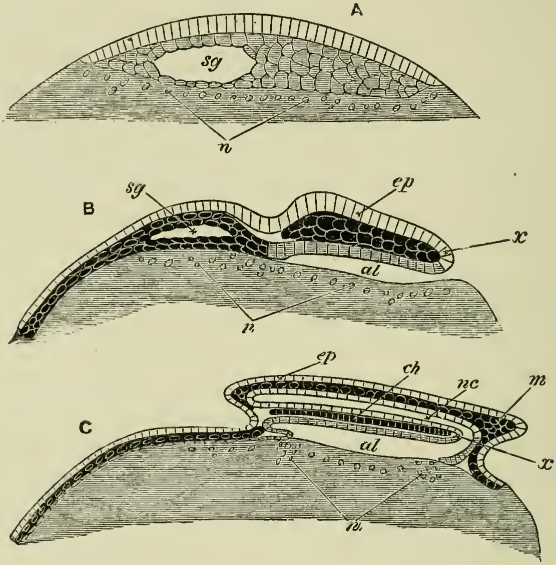
[1] *Archiv f. Mikr. Anat.* Vol. XXI.

[2] Comparison, &c., *Quart. Journ. Micr. Science*, July, 1875.

interest. An answer to it has already been attempted from a general point of view in my paper[1] entitled 'The Comparison of the early stages of development in Vertebrates'; but the subject may be conveniently treated here in a special manner for Elasmobranch embryos.

In the wood-cut, fig. 1 *A*, *B*, *C*[2], are represented three diagrammatic longitudinal sections of an Elasmobranch embryo.

FIG. 1.



Diagrammatic longitudinal sections of an Elasmobranch embryo.

Epiblast without shading. *Mesoblast* black with clear outlines to the cells. *Lower layer cells* and *hypoblast* with simple shading.

ep. epiblast. *m.* mesoblast. *al.* alimentary cavity. *sg.* segmentation cavity. *nc.* neural canal. *ch.* notochord. *x.* point where epiblast and hypoblast become continuous at the posterior end of the embryo. *n.* nuclei of yolk.

A. Section of young blastoderm, with segmentation cavity in the middle of the lower layer cells.

B. Older blastoderm with embryo in which hypoblast and mesoblast are distinctly formed, and in which the alimentary slit has appeared. The segmentation cavity is still represented as being present, though by this stage it has in reality disappeared.

C. Older blastoderm with embryo in which neural canal has become formed, and is continuous posteriorly with alimentary canal. The notochord, though shaded like mesoblast, belongs properly to the hypoblast.

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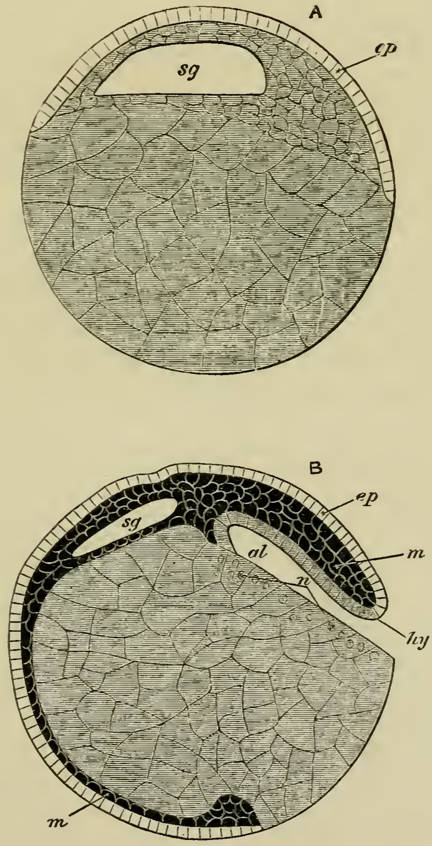
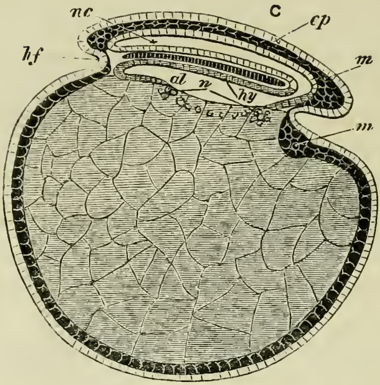
[1] *Loc. cit.*

[2] This figure, together with fig. 2 and 3, are reproduced from my paper upon the comparison of the early stages of development in vertebrates.

A nearly corresponds with the longitudinal section represented on Pl. III. fig. 4, and *B* with Pl. IV. fig. 7. In Pl. IV. fig. 7, the segmentation cavity has however completely disappeared, while it is still represented as present in the diagram of the same period. If these diagrams, or better still, the wood-cuts fig. 2 *A*, *B*, *C* (which only differ from those of the Elasmobranch fish in the smaller amount of food-yolk), be compared with the corresponding ones of Bombinator, fig. 3 *A*, *B*, *C*, they will be found to be in fundamental agreement with them. First let fig. 1 *A*, or fig. 2 *A*, or Pl. III. fig. 4, be compared

FIG. 2.





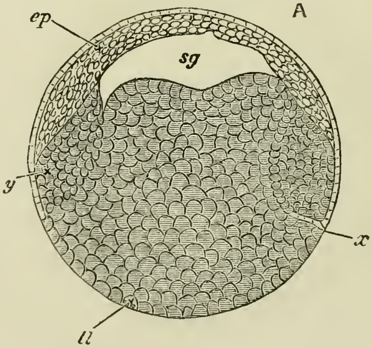
Diagrammatic longitudinal sections of embryo, which develops in the same manner as the Elasmobranch embryo, but in which the ovum contains far less food-yolk than is the case with the Elasmobranch ovum.

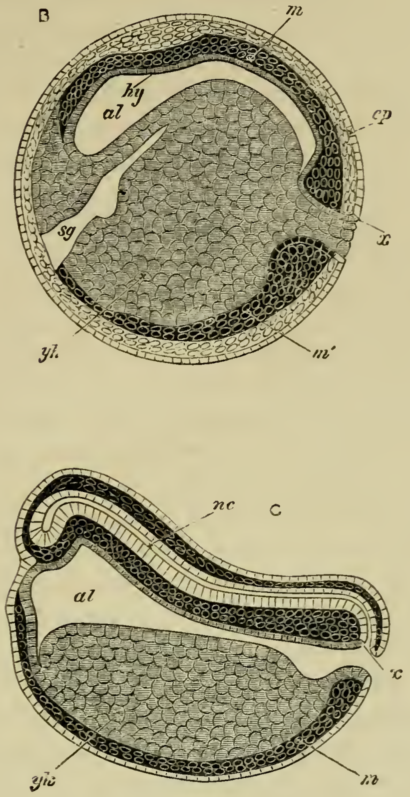
Epiblast without shading. *Mesoblast* black with clear outlines to the cells. *Lower layer cells* and *hypoblast* with simple shading.

ep. epiblast. *m.* mesoblast. *hy.* hypoblast. *sg.* segmentation cavity. *al.* alimentary cavity. *nc.* neural canal. *hf.* head-fold. *n.* nuclei of the yolk. The stages *A*, *B* and *C* are the same as in figure 1.

with fig. 3 *A*. In all there is present a segmentation cavity situated not centrally but near the surface of the egg. The roof of the cavity is thin in all, being composed in the Amphibian of epiblast alone, and in the Elasmobranch of epiblast and *lower layer cells.* The floor of the cavity is, in

FIG. 3.





Diagrammatic longitudinal sections of Bombinator igneus. Reproduced with modifications from Götte.

Epiblast without shading. *Mesoblast* black with clear outlines to the cells. *Lower layer cells* and *hypoblast* with single shading.

ep. epiblast. *l.l.* lower layer cells. *y.* smaller lower layer cells at the sides of the segmentation cavity. *m.* mesoblast. *hy.* hypoblast. *al.* alimentary cavity. *sg.* segmentation cavity. *nc.* neural cavity. *yk.* yolk-cells.

A is the youngest stage in which the alimentary involution has not yet appeared. *x* is the point from which the involution will start to form the dorsal wall of the alimentary tract. The line on each side of the segmentation cavity, which separates the smaller lower layer cells from the epiblast cells, is not present in Götte's original figure. The two shadings employed in the diagram render it necessary to have some line, but at this stage it is in reality not possible to assert which cells belong to the epiblast and which to the lower layer.

B. In this stage the alimentary cavity has become formed, but the segmentation cavity is not yet obliterated.

x. point where epiblast and hypoblast become continuous.

C. The neural canal is already formed, and communicates posteriorly with the alimentary.

x. point where epiblast and hypoblast become continuous.

all, formed of so-called yolk (*Vide* Pl. III. fig. 4), which in all forms the main mass of the egg. In the Amphibian the yolk is segmented, and, though it is not segmented in the Elasmobranch, it contains in compensation the nuclei so often mentioned. In all the sides of the segmentation cavity are formed by lower layer cells. In the Amphibian the sides are enclosed by smaller cells (in the diagram) which correspond exactly in function and position with the lower layer cells of the Elasmobranch blastoderm.

The relation of the yolk to the blastoderm in the Elasmobranch embryo at this stage of development very well suits the view of its homology with the large cells of the Amphibian ovum. The only essential difference between the two ova arises from the roof of the segmentation cavity being in the Elasmobranch embryo formed of lower layer cells, which are absent in the Amphibian embryo. This difference no doubt depends upon the greater quantity of yolk particles present in the Elasmobranch ovum. These increase the bulk of the lower layer cells, which are thus compelled to creep up the sides of the segmentation cavity till they close it in above.

In the next stage for the Elasmobranch, fig. 1 and 2 *B* and Pl. IV. fig. 7, and for the Amphibian, fig. 3 *B*, the agreement between the two types is again very close. In both for a small portion (x) of the edge of the blastoderm the epiblast and hypoblast become continuous, while at all other parts the epiblast, accompanied by lower layer cells, grows round the yolk or round the large cells which correspond to it. The yolk cells of the Amphibian ovum form a comparatively small mass, and are therefore rapidly enveloped; while in the case of the Elasmobranch ovum, owing to the greater mass of the yolk, the same process occupies a long period. In both ova the portion of the blastoderm, where epiblast and hypoblast become continuous, forms the dorsal lip of an opening—the anus of Rusconi—which leads into the alimentary cavity. This cavity has the same relation in both ova. It is lined dorsally by lower layer cells, and ventrally by yolk or what corresponds with yolk; the ventral epithelium of the alimentary canal being in both cases eventually supplied by the yolk cells.

As in the earlier stage, so in the present one, the anatomical relations of the yolk to the blastoderm in the one case (Elasmobranch) are nearly identical with those of the yolk cells to the blastoderm in the other (Amphibian). The main features in which the two embryos differ, during the stage under consideration, arise from the same cause as the solitary point of difference during the preceding stage.

In Amphibians, the alimentary cavity is formed coincidently with a true ingrowth of cells from the point where epiblast and hypoblast become continuous, and from this ingrowth the dorsal wall of the alimentary cavity is formed. The same ingrowth causes the obliteration of the segmentation cavity.

In the Elasmobranchs, owing to the larger bulk of the lower layer cells caused by the food-yolk, these have been compelled to arrange themselves in their final position during segmentation, and no room is left for a true invagination; but instead of this there is formed a simple split between the blastoderm and the yolk. The homology of this with the primitive invagination is nevertheless proved by the survival of a number of features belonging to the ancestral condition in which a true invagination was present. Amongst the more important of these are the following:—(1) The continuity of epiblast and hypoblast at the dorsal lip of the anus of Rusconi. (2) The continuous conversion of indifferent lower layer cells into hypoblast, which gradually extends backwards towards the segmentation cavity, and exactly represents the course of the invagination whereby in Amphibians the dorsal wall of the alimentary cavity is formed. (3) The obliteration of the segmentation cavity during the period when the pseudo-invagination is occurring.

The asymmetry of the gastrula or pseudo-gastrula in Cyclostomes, Amphibians, Elasmobranchs and, I believe, Osseous Fishes, is to be explained by the form of the vertebrate body. In Amphioxus, where the small amount of food-yolk present is distributed uniformly, there is no reason why the invagination and resulting gastrula should not be symmetrical. In other vertebrates, where more food-yolk is present, the shape and structure of the body render it necessary for the food-yolk to be stored away on the ventral side of the alimentary canal. This, combined with the unsymmetrical position of the anus, which primitively corresponds in position with the blastopore or anus of Rusconi, causes the asymmetry of the gastrula invagination, since it is not possible for the part of ovum which will become the ventral wall of the alimentary canal, and which is loaded with food-yolk, to be invaginated in the same fashion as the dorsal wall. From the asymmetry, so caused, follow a large number of features in vertebrate development, which have been worked out in some detail in my paper already quoted[1].

Prof. Haeckel, in a paper recently published[2], appears to imply that because I do not find absolute invagination in Elasmobranchs, I therefore look upon Elasmobranchs as militating against his Gastræa theory. I cannot help thinking that Prof. Haeckel must have somewhat misunderstood my meaning. The importance of the Gastræa theory has always appeared to me to consist not in the fact that an actual ingrowth of certain cells occurs—an ingrowth which might have many different meanings[3]—but in the fact that the types of early development of all animals can be easily derived from that of the typical gastrula. I am perfectly in accordance with Professor Haeckel in regarding the type of Elasmobranch development to be a simple derivative from that of the gastrula, although believing it to be without any true ingrowth or invagination of cells.

Professor Haeckel[4] in the paper just referred to published his view upon the mutual relationships of the various vertebrate blastoderms. In this paper, which appeared but shortly after my own[5] on the same subject, he has put forward views which differ from mine in several important details. Some of these bear upon the nature of food-yolk; and it appears to me that Professor Haeckel's scheme of development is incompatible with the view that the food-yolk in meroblastic eggs is the homologue of part of the hypoblast of the holoblastic eggs.

The following is Professor Haeckel's own statement of the

[1] *Quart. Journ. of Micr. Science*, July, 1875.

[2] Die Gastrula u. Eifurchung d. Thiere, *Jenaische Zeitschrift*, Vol. IX.

[3] For instance, in Crustaceans it does not in some cases appear certain whether an invagination is the typical gastrula invagination, or only an invagination by which, at a period subsequent to the gastrula invagination, the hind gut is frequently formed.

[4] *Loc. cit.*

[5] *Loc. cit.*

scheme or type, which he regards as characteristic of meroblastic eggs, pp. 98 and 99.

Jetzt folgt der höchst wichtige und interessante Vorgang, den ich als Einstülpung der Blastula auffasse und der zur Bildung der Gastrula führt (Fig. 63, 64)[1]. Es schlägt sich nämlich der verdickte Saum der Keimscheibe, der "Randwulst" oder das *Properistom*, nach innen um und eine dünne Zellenschicht wächst als directe Fortsetzung desselben, wie ein immer enger werdendes Diaphragma, in die Keimhöhle hinein. Diese Zellenschicht ist das entstehende Entoderm (Fig. 64 *i*, 74 *i*). Die Zellen, welche dieselbe zusammensetzen und aus dem innern Theile des Randwulstes hervorwachsen, sind viel grösser aber flacher als die Zellen der Keimhöhlendecke und zeigen ein dunkleres grobkörniges Protoplasma. Auf dem Boden der Keimhöhle, d. h. also auf der Eiweisskugel des Nahrungsdotters, liegen sie unmittelbar auf und rücken hier durch centripetale Wanderung gegen dessen Mitte vor, bis sie dieselbe zuletzt erreichen und nunmehr eine zusammenhängende einschichtige Zellenlage auf dem ganzen Keimhöhlenboden bilden. Diese ist die erste vollständige Anlage des Darmblatts, Entoderms oder "Hypoblasts", und von nun an können wir, im Gegensatz dazu den gesammten übrigen Theil des Blastoderms, nämlich die mehrschichtige Wand der Keimhöhlendecke als Hautblatt, Exoderm oder "Epiblast" bezeichnen. Der verdickte Randwulst (Fig. 64 *w*, 74 *w*), in welchem beide primäre Keimblätter in einander übergehen, besteht in seinem oberen und äusseren Theile aus Exodermzellen, in seinem unteren und inneren Theile aus Entodermzellen.

In diesem Stadium entspricht unser Fischkeim einer Amphiblastula, welche mitten in der Invagination begriffen ist, und bei welcher die entstehende Urdarmhöhle eine grosse Dotterkugel aufgenommen hat. Die Invagination wird nunmehr dadurch vervollständigt und die Gastrulabildung dadurch abgeschlossen, dass die Keimhöhle verschwindet. Das wachsende Entoderm, dem die Dotterkugel innig anhängt, wölbt sich in die letztere hinein und nähert sich so dem Exoderm. Die klare Flüssigkeit in der Keimhöhle wird resorbirt und schliesslich legt sich die obere convexe Fläche des Entoderms an die untere concave des Exoderms eng an: die Gastrula des discoblastischen Eies oder die "Discogastrula" ist fertig (Fig. 65, 76; Meridiandurchschnitt Fig 66, 75).

Die Discogastrula unsers Knochenfisches in diesem Stadium der vollen Ausbildung stellt nunmehr eine kreisrunde Kappe dar, welche wie ein gefüttertes Mützchen fast die ganze obere Hemisphäre der hyalinen Dotterkugel eng anliegend bedeckt (Fig. 65). Der Ueberzug des Mützchens entspricht dem Exoderm (*e*), sein Futter dem Entoderm (*i*). Ersteres besteht aus drei Schichten von kleineren Zellen, letzteres aus einer einzigen Schicht von grösseren Zellen. Die Exodermzellen (Fig. 77) messen 0,006—0,009 Mm., und haben ein klares, sehr feinkörniges Protoplasma. Die Entodermzellen (Fig.

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[1] The references in this quotation are to the figures in the original.

78) messen 0,02—0,03 Mm. und ihr Protoplasma ist mehr grobkörnig und trüber. Letztere bilden auch den grössten Theil des Randwulstes, den wir nunmehr als Urmundrand der Gastrula, als "*Properistoma*" oder auch als "RUSCONI'schen After" bezeichnen können. Der letztere umfasst die Dotterkugel, welche die ganze Urdarmhöhle ausfüllt und weit aus der dadurch verstopften Urmund-Oeffnung vorragt.

My objections to the view so lucidly explained in the passage just quoted, fall under two heads.

(1) That the facts of development of the meroblastic eggs of vertebrates, are not in accordance with the views here advanced.

(2) That even if these views be accepted as representing the actual facts of development, the explanation offered of these facts would not be satisfactory.

Professor Haeckel's views are absolutely incompatible with the facts of Elasmobranch development, if my investigations are correct.

The grounds of the incompatibility may be summed up under the following heads:

(1) In Elasmobranchs the hypoblast cells occupy, even before the close of segmentation, the position which, on Professor Haeckel's view, they ought only eventually to take up after being involuted from the whole periphery of the blastoderm.

(2) There is no sign at any period of an invagination of the periphery of the blastoderm, and the only structure (the embryonic rim) which could be mistaken for such an invagination is confined to a very limited arc.

(3) The growth of cells to form the floor of the segmentation cavity, which ought to be part of this general invagination from the periphery, is mainly due to a formation of cells from the yolk.

It is this ingrowth of cells for the floor of the segmentation cavity which, I am inclined to think, Professor Haeckel has mistaken for a general invagination in the Osseous Fish he has investigated.

(4) Professor Haeckel fails to give an account of the asymmetry of the blastoderm; an asymmetry which is unquestion-

ably also present in the blastoderm of most Osseous Fishes, though not noticed by Professor Haeckel in the investigations recorded in his paper.

The facts of development of Osseous Fishes, upon which Professor Haeckel rests his views, are too much disputed, for their discussion in this place to be profitable[1]. The eggs of Osseous Fishes appear to me unsatisfactory objects for the study of this question, partly on account of all the cells of the blastoderm being so much alike, that it is a very difficult matter to distinguish between the various layers, and, partly, because there can be little question that the eggs of existing Osseous Fishes are very much modified, through having lost a great part of the food-yolk possessed by the eggs of their ancestors[2]. This disappearance of the food-yolk must, without doubt, have produced important changes in development, which would be especially marked in a pelagic egg, like that investigated by Professor Haeckel.

The Avian egg has been a still more disputed object than even the egg of the Osseous Fishes. The results of my own investigations on this subject do not accord with those of Dr Götte, or the views of Professor Haeckel[3].

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[1] A short statement by Kowalevsky on this subject in a note to his account of the development of Ascidians, would seem to indicate that the type of development of Osseous Fishes is precisely the same as that of Elasmobranchs. Kowalevsky says, *Arch. f. Micr. Anat.* Vol. VII. p. 114, note 5. "According to my observations on Osseous Fishes the germinal wall consists of two layers, an upper and lower, which are continuous with one another at the border. From the upper one develops skin and nervous system, from the lower hypoblast and mesoblast." This statement, which leaves unanswered a number of important questions, is too short to serve as a basis for supporting my views, but so far as it goes its agreement with the facts of Elasmobranch development is undoubtedly striking.

[2] The eggs of the Osseous Fishes have, I believe, undergone changes of the same character, but not to the same extent, as those of Mammalia, which, according to the views expressed both by Professor Haeckel and myself, are degenerated from an ovum with a large food-yolk. The grounds on which I regard the eggs of Osseous Fishes as having undergone an analogous change, are too foreign to the subject to be stated here.

[3] I find myself unable without figures to understand Dr Rauber's (*Centralblatt für Med. Wiss.* 1874, No. 50; 1875, Nos. 4 and 17) views with sufficient precision to accord to them either my assent or dissent. It is quite in accordance with the view propounded in my paper (*loc. cit.*) to regard, with Dr Rauber and Professor Haeckel, the thickened edge of the blastoderm as the homologue of the lip of the blastopore in Amphioxus; though an invagination, in the manner imagined by Professor Haeckel, is no necessary consequence of this view. If Dr Rauber regards the *whole* egg of the bird as the homologue of that of Amphioxus, and the inclosure of the yolk by the blastoderm as the equivalent to the process of invagination in Amphioxus, then his views are practically in accordance with my own.

Apart from disputed points of development, it appears to me that a comparative account of the development of the meroblastic vertebrate ova ought to take into consideration the essential differences which exist between the Avian and Piscian blastoderms, in that the embryo is situated in the centre of the blastoderm in the first case and at the edge in the second[1].

This difference entails important modifications in development, and must necessarily affect the particular points under discussion. As a result of the different positions of the embryo in the two cases, there is present in Elasmobranchs and Osseous Fishes a true anus of Rusconi, or primitive opening into the alimentary canal, which is absent in Birds. Yet in neither Elasmobranchs[2] nor Osseous Fishes does the anus of Rusconi correspond in position with the point where the final closing in of the yolk takes place, but in them this point corresponds rather with the blastopore of Birds[3].

Owing also to the respective situations of the embryo in the blastoderm, the alimentary and neural canals communicate

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[1] I have suggested in a previous paper ("*Comparison*," &c., *Quart. Journal of Micr. Science*, July, 1875) that the position occupied by the embryo of Birds at the centre, and not at the periphery, of the blastoderm may be due to an abbreviation of the process by which the Elasmobranch embryos cease to be situated at the edge of the blastoderm (*vide* p. 81 and Pl. VIII. fig. 1, 2). Assuming this to be the real explanation of the position of the embryo in Birds, I feel inclined to repeat a speculation which I made some time ago with reference to the primitive streak in Birds (*Quart. Journ. of Micr. Science*, 1873, p. 280). In Birds there is, as is well known, a structure called the primitive streak, which has been shown by the observations of Dursy, corroborated by my observations (*loc. cit.*), to be situated behind the medullary groove, and to take no part in the formation of the embryo. I further showed that the peculiar fusion of epiblast and mesoblast, called by His the axis cord, was confined to this structure and did not occur in other parts of the blastoderm. Nearly similar results have been recently arrived at by Hensen with reference to the primitive streak in Mammals. The position of the primitive streak immediately behind the embryo suggests the speculation that it may represent the line along which the edges of the blastoderm coalesced, so as to give to the embryo the central position which it has in the blastoderms of Birds and Mammals, and that the peculiar fusion of epiblast and mesoblast at this point may represent the primitive continuity of epiblast and lower layer cells at the dorsal lip of the anus of Rusconi in Elasmobranchs. I put this speculation forwards as a mere suggestion, in the hope of elucidating the peculiar structure of the primitive streak, which not improbably may be found to be the keystone to the nature of the blastoderm of the higher vertebrates.

[2] *Vide* p. 81 and Plate VIII. fig. 1 and 2, and Self, "*Comparison*," &c., *loc. cit.*

[3] The relation of the anus of Rusconi and blastopore in Elasmobranchs was fully explained in the paper above quoted. It was there clearly shown that neither the one nor the other exactly corresponds with the blastopore of Amphioxus, but that the two together do so. Professor Haeckel states that in the Osseous Fish investigated by him the anus of Rusconi and the blastopore coincide. This is not the case in the Salmon.

posteriorly in Elasmobranchs and Osseous Fishes, but *not* in Birds. Of all these points Professor Haeckel makes no mention.

The support of his views which Prof. Haeckel attempts to gain from Götte's researches in Mammalia is completely cut away by the recent discoveries of Van Beneden[1] and Hensen[2].

It thus appears that Professor Haeckel's views but ill accord with the facts of vertebrate development; but even if they were to do so completely it would not in my opinion be easy to give a rational explanation of them.

Professor Haeckel states that no sharp and fast line can be drawn between the types of 'unequal' and 'discoidal' segmentation[3]. In the cases of unequal segmentation he admits, as is certainly the case, that the larger yolk cells (hypoblast) are simply enclosed by a growth of the epiblast around them; which is to be looked on as a modification of the typical gastrula invagination, necessitated by the large size of the yolk cells (*vide* Professor Haeckel's paper, Taf. II. fig. 30). In these instances there is no commencement of an ingrowth in the *manner supposed for meroblastic ova.*

When the food-yolk becomes more bulky, and the hypoblast does not completely segment, it is not easy to understand why an ingrowth, which had no existence in the former case, should occur; nor where it is to come from. Such an ingrowth as is supposed to exist by Professor Haeckel would, in fact, break the continuity of development between meroblastic and holoblastic ova, and thus destroy one of the most important results of the Gastræa theory.

It is quite easy to suppose, as I have done, that in the cases of discoidal segmentation, the hypoblast (including the yolk) becomes enclosed by the epiblast in precisely the same manner as in the cases of unequal segmentation.

But even if Professor Haeckel supposes that in the unsegmented food-yolk a fresh element is added to the ovum, it remains quite unintelligible to me how an ingrowth of cells from a circumferential line, to form a layer which had no previous

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[1] *Développement Embryonnaire des Mammifères, Bulletin de l'Acad. r. d. Belgique*, 1875.

[2] *Loc. cit.*

[3] For an explanation of these terms, *vide* Prof. Haeckel's original paper or the abstract in *Quart. Journ. of Micr. Science* for January, 1876.

existence, can be equivalent to, or derived from, the invagination of a layer, which exists before the process of invagination begins, and which remains continuous throughout it.

If Professor Haeckel's views should eventually turn out to be in accordance with the facts of vertebrate development, it will, in my opinion, be very difficult to reduce them into conformity with the Gastræa theory.

Although some space has been devoted to an attempt to refute the views of Professor Haeckel on this question, I wish it to be clearly understood that my disagreement from his opinions concerns matters of detail only, and that I quite accept the Gastræa theory in its general bearings.

Observations upon the formation of the layers in Elasmobranchs have hitherto been very few in number. Those published in my preliminary account of these fishes are, I believe, the earliest[1].

Since then there has been published a short notice on the subject by Dr Alex. Schultz[2]. His observations in the main accord with my own. He apparently speaks of the nuclei of the yolk as cells, and also of the epiblast being more than one cell deep. In Torpedo alone, amongst the genera investigated by me, is the layer of epiblast, at about the age of the last described embryo, composed of more than a single row of cells.

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[1] I omit all reference to a paper published in Russian by Prof. Kowalevsky. Being unable to translate it, and the illustrations being too meagre to be in themselves of much assistance, it has not been possible for me to make any use of it.

[2] *Centralblatt f. Med. Wiss.* No. 33, 1875.

CHAPTER IV.

THE GENERAL FEATURES OF THE ELASMOBRANCH EMBRYO AT SUCCESSIVE STAGES.

No complete series of figures, representing the various stages in development of an Elasmobranch Embryo, has hitherto been published. With the view of supplying this deficiency Plates VI. and VII. have been inserted. The embryos represented in these two Plates form a fairly complete series, but do not all belong to a single species. Those on Pl. VI., with the exception of G, are embryos of Pristiurus; G being an embryo of Torpedo. Those on Pl. VII., excepting K, which is a Pristiurus embryo, are embryos of Scyllium canicula. All the embryos on Pl. VII. were very accurately drawn from nature by my sister, Miss A. B. Balfour. Unfortunately the exceptional beauty and clearness of the originals is all but lost in the lithographs. To facilitate future description, letters will be employed in the remainder of these pages to signify that an embryo being described is of the same age as the embryo on these Plates to which the letter used refers. Thus an embryo of the same age as L will be spoken of hereafter as belonging to stage L.

A.

This figure represents a hardened blastoderm at a stage when the embryo-swelling (*e. s.*) has become obvious, but before the appearance of the medullary groove. The position of the segmentation cavity is indicated by a slight swelling of the blastoderm (*s. c.*). The shape of the blastoderm, in hardened specimens, is not to be relied upon, owing to the traction which the blastoderm undergoes during the process of removing the yolk from the egg-shell.

B.

B is the view of a fresh blastoderm. The projecting part of this, already mentioned as the 'embryonic rim', is indicated by the shading. At the middle of the embryonic rim is to be seen the rudiment of the embryo (*m. g.*). It consists of an area of the blastoderm, circumscribed on its two sides and at one end, by a slight fold, and whose other end forms part of the edge of the blastoderm. The end of the embryo which points towards the *centre* of the blastoderm is the head end, and that which forms part of the *edge* of the blastoderm is the tail end. To retain the nomenclature usually adopted in treating of the development of the Bird, the fold at the anterior end of the embryo may be called *the head fold,* and those at the sides the *side folds.* There is in Elasmobranchs no tail fold, owing to the position of the embryo at the periphery of the blastoderm, and it is by the meeting of the three above-mentioned folds only, that the embryo becomes pinched off from the remainder of the blastoderm. Along the median line of the embryo is a shallow groove (*m. g.*), the well-known medullary groove of vertebrate embryology. It flattens out both anteriorly and posteriorly, and is deepest in the middle part of its course.

C.

This embryo resembles in most of its features the embryo last described. It is, however, considerably larger, and the head-fold and side-folds have become more pronounced structures. The medullary groove is far deeper than in the earlier stage, and widens out anteriorly. This anterior widening is the first indication of a distinction between the brain and the remainder of the central nervous system, a distinction which arises long before the closure of the medullary canal.

D.

This embryo is far larger than the one last described, but the increase in length does not cause it to project beyond the edge of the blastoderm, but has been due to a growth inwards towards the centre of the blastoderm. The head is now indicated by an anterior enlargement, and the embryo also widens out posteriorly. The posterior widening (*t. s.*) is formed by a pair of rounded prominences, one on each side of the middle line. These are very conspicuous organs during the earlier stages of development, and consist of two large aggregations of mesoblast cells. In accordance with the nomenclature adopted in my preliminary paper[1], they may be called 'tail-swellings'. Between the cephalic enlargements and the tail-swellings is situated the rudimentary trunk of the embryo. It is more completely pinched off from the blastoderm than in the last described embryo. The medullary groove is of a fairly uniform size throughout the trunk of the embryo, but flattens out and vanishes completely in the region of the head. The blastoderm in Pristiurus and Scyllium grows very rapidly, and has by this stage attained a very considerable size; but in Torpedo its growth is very slow.

E and F.

These two embryos may be considered together, for, although they differ in appearance, yet they are of an almost identical age; and the differences between the two are purely external. E appears to be a little abnormal in not having the cephalic region so distinctly marked off from the trunk as is usual. The head is proportionally larger than in the last stage, and the tail-swellings remain as conspicuous as before. The folding off from the blastoderm has progressed rapidly, and the head and tail are quite separated from it. The medullary groove has become closed posteriorly in both embryos, but the closing has extended further forwards in F than in E. In F the medullary folds have not only united posteriorly, but have very nearly effected a fresh junction in the region of the neck. At this point a second junction of the two medullary folds is in fact actually effected before the posterior closing has extended forwards so far. The later junction in the region of the neck corresponds in position with the point, where in the Bird the medullary folds first unite. No trace of a medullary groove is to be met with in the head, which simply consists of a wide flattened plate. Between the two tail-swellings surface views present the appearance of a groove, but this appearance is deceptive, since in sections no groove, or at most a very slight one, is perceptible.

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[1] *Quart. Journ. Micr. Science*, Oct. 1874.

G.

During the preceding stages growth in the embryo is very slow, and considerable intervals of time elapse before any perceptible changes are effected. This state of things now becomes altered, and the future changes succeed each other with far greater rapidity. One of the most important of these, and one which first presents itself during this stage, is the disappearance of the yolk spherules from the embryonic cells, and the consequently increased transparency of the embryo. As a result of this, a number of organs, which in the earlier stages were only to be investigated by means of sections, now become visible in the living embryo.

The tail-swellings (*t. s.*) are still conspicuous objects at the posterior extremity of the embryo. The folding off of the embryo from the yolk has progressed to such an extent that it is now quite possible to place the embryo on its side and examine it from that point of view.

The embryo may be said to be attached to the yolk by a distinct stalk or cord, which in the succeeding stages gradually narrows and elongates, and is known as the umbilical cord (*so. s.*). The medullary canal has now become completely closed, even in the region of the brain, where during the last stage no trace of a medullary groove had appeared. Slight constrictions, not perceptible in views of the embryo as a transparent object, mark off three vesicles in the brain. These vesicles are known as the fore, mid, and hind brain. From the fore-brain there is an outgrowth on each side, the first rudiment of the optic vesicle (*op.*).

The mesoblast on each side of the body is divided into a series of segments, known as protovertebræ or muscle-plates, the first of which lies a little behind the head. The mesoblast of the tail has not as yet undergone this segmentation. There are present in all seventeen segments. These first appeared at a much earlier date, but were not visible owing to the opacity of the embryo.

Another structure which became developed in even a younger embryo than C is now for the first time visible in the living embryo. This is the notochord: it extends from almost the extreme posterior to the anterior end of the embryo. It lies between the ventral wall of the spinal canal and the dorsal wall of the intestine; and round its posterior end these two walls become continuous with each other (*vide* fig.). Anteriorly the termination of the notochord cannot be seen, it can only be traced into a mass of mesoblast at the base of the brain, which there separates the epiblast from the hypoblast. The alimentary canal (*al.*) is completely closed anteriorly and posteriorly, though still widely open to the yolk-sac in the middle part of its course. In the region of the head it exhibits on each side a slight bulging outwards, the rudiment of the first visceral cleft. This is represented in the figure by two lines (I *v.c.*). The visceral clefts at this stage consist of a pair of simple diverticula from the alimentary canal, and there is no communication between the throat and the exterior.

H.

The present embryo is far larger than the last, but it has not been possible to represent this increase in size in the drawings. Accompanying this increase in size, the folding off of the embryo from the yolk has considerably progressed, and the stalk which unites the embryo with the yolk is proportionately narrower and longer than before.

The brain is now very distinctly divided into the three lobes, whose rudiments appeared during the last stage. From the foremost of these, the optic vesicles now present themselves as well-marked lateral outgrowths, towards which there appears a growing in, or involution, from the external skin (*op.*) to form the lens. The opening of this involution is represented by the dark spot in the centre.

A fresh organ of sense, the auditory sac, now for the first time becomes visible as a shallow pit in the external skin on each side of the hind-brain (*au. v.*). The epiblast which is involuted to form this pit becomes much thickened, and thereby the opacity, indicated in the figure, is produced.

The muscle-plates have greatly increased in number by the formation of fresh segments in the tail. Thirty-eight of them were present in the embryo figured. The mesoblast at the base of the brain has increased in quantity, and there is still a certain mass of unsegmented mesoblast which forms the tail-swellings. The first rudiment of the heart becomes visible during this stage as a cavity between the mesoblast of the splanchnopleure and the hypoblast (*ht.*).

The fore and hind guts are now longer than they were. A slight pushing in from the exterior to form the mouth has appeared (*m.*), and an indication of the future position of the anus is afforded by a slight diverticulum of the hind gut towards the exterior some little distance from the posterior end of the embryo (*an.*). The portion of the alimentary canal behind this point, though at this stage large, and even dilated into a vesicle at its posterior end (*al. v.*), becomes eventually completely atrophied. In the region of the throat the rudiment of a second visceral cleft has appeared behind the first; neither of them are as yet open to the exterior. The number of visceral clefts present in any given Pristiurus embryo affords a very easy and simple way of determining its age.

I.

A great increase in size is again to be noticed in the embryo, but, as in the case of the last embryo, it has not been possible to represent this in the figure. The stalk connecting the embryo with the yolk has become narrower and more elongated, and the tail region of the embryo proportionately far longer than in the last stage. During this stage the first spontaneous movements of the embryo take place, and consist in somewhat rapid excursions of the embryo from side to side, produced by a serpentine motion of the body.

The cranial flexure, which commenced in stage G, has now become very evident, and the mid-brain[1] begins to project in the same manner as in the embryo fowl on the third day, and will soon form the anterior termination of the long axis of the embryo. The fore-brain has increased in size and distinctness, and the anterior part of it may now be looked on as the impaired rudiment of the cerebral hemispheres.

Further growths have taken place in the organs of sense,

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[1] The part of the brain which I have here called mid-brain, and which unquestionably corresponds to the part called mid-brain in the embryos of higher vertebrates, becomes in the adult what Miklucho-Maclay and Gegenbaur called the vesicle of the third ventricle or thalamencephalon. I shall always speak of it as the mid-brain.

especially in the eye, in which the involution for the lens has made considerable progress. The number of the muscle-plates has again increased, but there is still a region of unsegmented mesoblast in the tail. The thickened portions of mesoblast which caused the tail-swellings are still to be seen and would seem to act as the reserve from which is drawn the matter for the rapid growth of the tail, which occurs soon after this. The mass of the mesoblast at the base of the brain has again increased. No fresh features of interest are to be seen in the notochord. The heart is now much more conspicuous than before, and its commencing flexure is very apparent. It now beats actively. The hind gut especially is much longer than in the last specimen; and the point where the anus will appear is very easily detected by the bulging out of the gut towards the external skin at that point (*an.*). The alimentary vesicle, first observable during the last stage, is now a more conspicuous organ (*al. v.*). Three visceral clefts, none of which are as yet open to the exterior, may now be seen.

K.

The figures G, H, I are representations of living and transparent embryos, but the remainder of the figures are drawings of opaque embryos which were hardened in chromic acid.

The stalk connecting the embryo with the yolk is now, comparatively speaking, quite narrow, and is of sufficient length to permit the embryo to execute considerable movements.

The tail has grown immensely, but is still dilated terminally. This terminal dilatation is mainly due to the alimentary vesicle, but the tract of gut connecting this with the gut in front of the anus is now a solid rod of cells and very soon becomes completely atrophied.

The two pairs of limbs have appeared as elongated ridges of epiblast. The anterior pair is situated just at the front end of the umbilical stalk; and the posterior pair, which is the more conspicuous of the two, is situated some little distance behind the stalk.

The cranial flexure has greatly increased, and the angle between the long axis of the front part of the head and of the body is less than a right angle. The conspicuous mid-brain forms the anterior termination of the long axis of the body. The thin roof of the fourth ventricle may in the figure be noticed behind the mid-brain. The auditory sac is nearly closed and its opening is not shown in the figure. In the eye the lens is completely formed.

Owing to the opacity of the embryo, the muscle-plates are only indistinctly indicated, and no other features of the mesoblast are to be seen.

The mouth is now a deep pit, whose borders are almost completely formed by the thickening in front of the first visceral cleft, which may be called the first visceral arch or mandibular arch.

Four visceral clefts are now visible, all of which are open to the exterior, but in a transparent embryo one more, not open to the exterior, would have been visible behind the last of these.

L.

This embryo is considerably older than the one last described, but growth is not quite so rapid as might be gathered from the fact that L is nearly twice as long as K, since the two embryos belong to different genera; and the Scyllium embryos, of which L is an example, are larger than Pristiurus embryos. The umbilical stalk is now quite a narrow elongated structure, whose subsequent external changes are very unimportant, and consist for the most part merely in an increase in its length.

The tail has again grown greatly in length, and its terminal dilatation together with the alimentary vesicle contained in it, have both completely vanished. A dorsal and ventral fin are now clearly visible; they are continuous throughout their whole length. The limbs have grown and are more easily seen than in the previous stage.

Great changes have been effected in the head, resulting in a diminution of the cranial flexure. This diminution is nevertheless apparent rather than real, and is chiefly due to the rapid growth of the rudiment of the cerebral hemispheres. The three main divisions of the brain may still be clearly seen from the surface. Posteriorly is situated the hind-brain, now consisting of the medulla oblongata and cerebellum. At the anterior part of the medulla is to be seen the thin roof of the fourth ventricle, and anteriorly to this again the roof becomes thickened to form the rudiment of the cerebellum. In front of the hind-brain lies the mid-brain, the roof of which is formed by the optic lobes, which are still situated at the front end of the long axis of the embryo.

Beyond the mid-brain is placed the fore-brain, whose growth is rapidly rendering the cranial flexure imperceptible.

The rudiments of the nasal sacs are now clearly visible as a pair of small pits. The pits are widely open to the exterior, and are situated one on each side, near the front end of the cerebral hemispheres. Five visceral clefts are open to the exterior, and in them the external gills have commenced to appear (L′).

The first cleft is no longer similar to the rest, but has commenced to be metamorphosed into the spiracle.

Accompanying the change in position of the first cleft, the mandibular arch has begun to bend round and enclose the front as well as the side of the mouth. By this change in the mandibular arch the mouth becomes narrowed in an antero-posterior direction.

M.

Of this embryo the head alone has been represented. Two views of it are given, one (M) from the side and the other (M′) from the under surface. The growth of the front part of the head has considerably diminished the prominence of the cranial flexure. The full complement of visceral clefts is now present—six in all. But the first has already atrophied considerably, and may easily be recognised as the spiracle. In Scyllium, there are present at no period more than six visceral clefts. The first visceral arch on each side has become bent still further round, to form the front border of the mouth. The opening of the mouth has in consequence become still more narrowed in an antero-posterior direction. The width of the mouth in this direction, serves for the present and for some of the subsequent stages as a very convenient indication of age.

N.

The limbs, or paired fins, have now acquired the general features and form which they possess in the adult.

The unpaired fins have now also become divided in a manner not only characteristic of the Elasmobranchs but even of the genus Scyllium.

There is a tail fin, an anal fin and two dorsal fins, both the latter being situated behind the posterior paired fins.

In the head may be noticed a continuation of the rapid growth of the anterior part.

The mouth has become far more narrow and slit-like; and with many other of the organs of the period commences to approach the form of the adult.

The present and the three preceding stages show the gradual changes by which the first visceral arch becomes converted into the rudiments of the upper and of the lower jaw. The fact of the conversion was first made known through the investigations of Messrs Parker and Gegenbaur.

O.

In this stage the embryo is very rapidly approaching the form of the adult.

This is especially noticeable in the fins, which project in a manner quite characteristic of the adult fish. The mouth is slit-like, and the openings of the nasal sacs no longer retain their primitive circular outline. The external gills project from all the gill-slits including the spiracle.

P.

The head is rapidly elongating by the growth of the snout, and the divisions of the brain can no longer be seen with distinctness from the exterior, and, with the exception of the head and of the external gills, the embryo almost completely resembles the adult.

Q.

The snout has grown to such an extent, that the head has nearly acquired its adult shape. In the form of its mouth the embryo now quite resembles the adult fish.

This part of the subject may be conveniently supplemented by a short description of the manner in which the blastoderm encloses the yolk. It has been already mentioned that the growth of the blastoderm is not uniform. The part of it in the immediate neighbourhood of the embryo remains comparatively stationary, while the growth elsewhere is very rapid. From this it results that that part of the edge of the blastoderm where the embryo is attached forms a bay in the otherwise regular outline of the edge of the blastoderm. By the time that one-half of the yolk is enclosed the bay is a very conspicuous feature (Pl. VIII. fig. 1). In this figure *bl.* points to the blastoderm, and *yk.* to the part of the yolk not yet enclosed by the blastoderm.

Shortly subsequent to this the bay becomes obliterated by its two sides coming together and coalescing, and the embryo ceases to lie at the edge of the yolk.

This stage is represented on Pl. VIII. fig. 2. In this figure there is only a small patch of yolk not yet enclosed (*yk*), which is situated at some little distance behind the embryo. Throughout all this period the edge of the blastoderm has remained thickened, a feature which persists till the complete investment of the yolk, which takes places shortly after the stage last figured. In this thickened edge a circular vein arises, which brings back the blood from the yolk-sac to the embryo. The opening in the blastoderm (Pl. VIII. fig. 2 *yk.*), exposing the portion of the yolk not yet enclosed, may be conveniently called the blastopore, according to Professor Lankester's nomenclature.

The interesting feature which characterizes the blastopore in Elasmobranchs is the fact of its not corresponding in position with the opening of the anus of Rusconi. We thus have in Elasmobranchs two structures, each of which corresponds in part with the single structure in Amphioxus which may be called either blastopore or anus of Rusconi, which yet do not in Elasmobranchs coincide in position. It is the blastopore of Elasmobranchs which has undergone a change of position, owing to the unequal growth of the blastoderm; while the anus of Rusconi retains its normal situation. In Osseous Fishes the blastopore undergoes a similar change of position. The possibility of a change in position of this structure is peculiarly interesting, in that it possibly serves to explain how the blastopore of different animals corresponds in different cases with the anus or the mouth, and has not always a fixed situation[1].

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[1] For a fuller discussion of this question *vide* Self, 'A comparison of the early stages of development in vertebrates.' *Quart. Journ. of Micr. Science*, July, 1875.

CHAPTER V.

Stages B to G.

THE present chapter deals with the history of the development of the Elasmobranch embryo from the period when the medullary groove first arises till that in which it becomes completely closed, and converted into the medullary canal. The majority of the observations recorded were made on Pristiurus embryos, a few on embryos of Torpedo. Where nothing is said to the contrary the statements made apply to the embryos of Pristiurus only.

The general external features for this period have already been given in sufficient detail in the last chapter; and I proceed at once to describe consecutively the history of the three layers.

General features of the Epiblast.

At the commencement of this period, during the stage intermediate between B and C, the epiblast is composed of a single layer of cells. (Pl. IX. fig. 1.)

These are very much elongated in the region of the embryo, but flattened in other parts of the blastoderm. Throughout they contain numerous yolk spherules.

In a Torpedo embryo of this age (as determined by the condition of the notochord) the epiblast presents a very different structure. It is composed of small spindle-shaped cells several rows deep. The nuclei of these are very large in proportion to the cells containing them, and the yolk spherules are far less numerous than in the cells of corresponding Pristiurus embryos.

During stage C the condition of the epiblast does not undergo any important change, with the exception of the layer becoming much thickened, and its cells two or three deep in the anterior parts of the embryo. (Pl. IX. fig. 2.)

In the succeeding stages that part of the epiblast, which will form the spinal cord, gradually becomes two or three cells deep. This change is effected by a decrease in the length of the cells as compared with the thickness of the layer. In the earlier stages the cells are wedge-shaped with an alternate arrangement, so that a decrement in the length of the cells at once causes the epiblast to be composed of two rows of interlocking cells.

The lateral parts of the epiblast which form the epidermis of the embryo are modified in quite a different manner to the nervous parts of the layer, becoming very much diminished in thickness and composed of a single row of flattened cells, Pl. IX. fig. 3.

Till the end of stage F, the epiblast cells and indeed all the cells of the blastoderm retain their yolk spherules, but the epiblast begins to lose them and consequently to become transparent in stage G.

Medullary Groove.

During stage B the medullary groove is shallow posteriorly, deeper in the middle part, and flattened out again at the extreme anterior end of the embryo. Pl. V. fig. 10, *a b c*.

A similar condition obtains in the stage between B and C, but the canal has now in part become deeper. Anteriorly no trace of it is to be seen. In stage C it exhibits the same general features (Plate IX. fig. 2*a* 2*b* 2*c*).

By stage D we find important modifications of the canal.

It is still shallow behind and deep in the dorsal region, Plate IX. fig. 3*d* 3*e* 3*f*; but the anterior flattened area in the last stage has grown into a round flat plate which may be called the cephalic plate, Plate VI. D and Plate IX. fig. 3*a* 3*b* 3*c*. This plate becomes converted into the brain. Its size and form give it a peculiar appearance, but the most remarkable feature about it is the ventral curvature of its edges. Its edges do not, as might be expected, bend dorsalwards towards each other, but become sharply bent in a ventral direction. This feature is for the first time apparent at this stage, but becomes more conspicuous during the succeeding ones, and attains its maximum in stage F (Plate IX. fig. 5), in which it mightal most be supposed that the edges of the cephalic plate were about to grow downwards and meet on the ventral side of the embryo.

In the stages subsequent to D the posterior part of the canal deepens much more rapidly than the rest (*vide* Pl. IX. fig. 4, taken from the posterior end of an embryo but slightly younger than F), and the medullary folds unite and convert the posterior end of the medullary groove into a closed canal (Pl. VI. fig. F), while the groove is still widely open elsewhere[1]. The medullary canal does not end blindly behind, but simply forms a tube not closed at either extremity. The importance of this fact will appear later.

In a stage but slightly subsequent to F nearly the whole of the medullary canal becomes formed. This occurs in the usual way by the junction and coalescence of the medullary folds. In the course of the closing of the medullary groove the edges of the cephalic plate lose their ventral curvature and become bent up in the normal manner (*vide* Pl. IX. fig. 6, a section taken through the posterior part of the cephalic plate), and the enlarged plate merely serves to enclose a dilated cephalic portion of the medullary canal. The closing of the medullary canal takes place earlier in the head and neck than in the back. The anterior end of the canal becomes closed and does not remain open like the posterior end.

Elasmobranch embryos resemble those of the Sturgeon (Acipenser) and the Amphibians in the possession of a spatula-like cephalic expansion: but so far as I am aware a ventral flexure in the medullary plates of the head has not been observed in other groups.

The medullary canal in Elasmobranchs is formed precisely on the type so well recognised for all groups of vertebrates with the exception of the Osseous Fishes. The only feature in any respect peculiar to these fishes is the closing of their medullary canal first commencing behind, and then at a second point in the cervical region. In those vertebrates in which the medullary folds do not unite at approximately the same time

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[1] *Vide* Preliminary Account, etc. *Q. Jl. Micros. Science*, Oct. 1874, Pl. XIV. 8 *a*. This and the other section from the same embryo (stage F) may be referred to. I have not thought it worth while repeating them here.

throughout their length, they appear usually to do so first in the region of the neck.

Mesoblast.

The separation from the hypoblast of two lateral masses of mesoblast has already been described. Till the close of stage C the mesoblast retains its primitive bilateral condition unaltered. Throughout the whole length of the embryo, with the exception of the extreme front part, there are present two plates of rounded mesoblast cells, one on each side of the medullary groove. These plates are in very close contact with the hypoblast, and also follow with fair accuracy the outline of the epiblast. This relation of the mesoblast plates to the epiblast must not however be supposed to indicate that the medullary groove is due to growth in the mesoblast: a view which is absolutely negatived by the manner of formation of the medullary groove in the head. Anteriorly the mesoblast plates thin out and completely vanish.

In stage D, the plates of mesoblast in the trunk undergo important changes. The cells composing them become arranged in two layers (Plate IX. fig. 3), a splanchnic layer adjoining the hypoblast (*sp*), and a somatic layer adjoining the epiblast[1] (*so*). Although these two layers are distinctly formed, they do not become separated at this stage in the region of the trunk, and in the trunk no true body-cavity is formed.

By stage D the plates of mesoblast have ceased to be quite isolated, and are connected with the lower layer cells of the general blastoderm.

Moreover the lower layer cells outside the embryo now exhibit distinct traces of a separation into two layers, one continuous with the hypoblast, the other with the mesoblast. Both layers are composed of very flattened cells, and the mesoblast layer is often more than one cell deep, and sometimes exhibits a mesh-like arrangement of its elements.

Coincidentally with the appearance of a differentiation into a somatic and splanchnic layer the mesoblast plates become

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[1] I under-estimated the distinctness of this formation in my earlier paper, *loc. cit.*, although I recognized the fact that the mesoblast cells became arranged in two distinct layers.

partially split by a series of transverse lines of division into protovertebræ. Only the proximal regions of the plates become split in this way, while their peripheral parts remain quite intact As a result of this each plate becomes divided into a proximal portion adjoining the medullary canal, which is divided into *proto-vertebræ,* and may be called the *vertebral plate,* and a peripheral portion not so divided, which may be called the *lateral plate.* These two parts are at this stage quite continuous with each other; and, as will be seen in the sequel, the body-cavity originally extends uninterruptedly to the summit of the vertebral plates.

By stage D at the least ten protovertebræ have appeared.

In Torpedo the mesoblast commences to be divided into two layers much earlier than in Pristiurus; and even before stage C this division is more or less clearly marked.

In the head and tail the condition of the mesoblast is by no means the same as in the body.

In the tail the plates of mesoblast become considerably thickened and give rise to two projections, one on each side, which have already been alluded to as caudal or tail-swellings; vide Pl. VI. figs. D, F, and Pl. IX. fig. 3 *f* and fig. 4 *ts.*

These masses of mesoblast are neither divided into protovertebræ, nor do they exhibit any trace of a commencing differentiation into somatopleure and splanchnopleure.

In the head, so far as I have yet been able to observe, the mesoblastic plates do *not* at this stage become divided into protovertebræ. The other changes exhibited in the cephalic region are of interest, mainly from the fact that here appears a cavity in the mesoblast directly continuous with the body-cavity (when that cavity becomes formed), but which appears at a very much earlier date than the body-cavity. This cavity can only be looked on in the light of a direct continuation of the body or peritoneal cavity into the head. Theoretical considerations with reference to it I propose reserving till I have described the changes which it undergoes in the subsequent periods.

Pl. IX. figures 3*a*, 3*b* and 3*c* exhibit very well the condition of the mesoblast in the head at this period. In fig. 3*c*, a section taken through the back part of the head. The mesoblast plates have nearly the same form as in the sections immediately behind. The ventral continuation of the mesoblast formed by the lateral plate has, however, become much thinner, and the dorsal or vertebral portion has acquired a more triangular form than in the sections through the trunk (fig. 3*d* and 3*e*).

In the section (fig. 3*b*) in front of this the ventral portion of the plate is no longer present, and only that part exists which corresponds with the vertebral division of the primitive plate of mesoblast.

In this a distinct cavity, forming part of the body cavity, has appeared.

In a still anterior section, fig. 3*a*, no cavity is any longer present in the mesoblast; whilst in sections taken from the foremost part of the head no mesoblast is to be seen (vide Pl. IX. fig. 5, taken from the front part of the head of the embryo represented in Pl. VI. fig. F).

A continuation of the body-cavity into the head has already been described by Oellacher[1] for the Trout: but he believes that the cavity in this part is solely related to the formation of the pericardial space.

The condition of the mesoblast undergoes no important change till the end of the period treated of in this chapter. The masses of mesoblast which form the tail-swellings become more conspicuous (Pl. IX. fig. 4); and indeed their convexity is so great that the space between them has the appearance of a median groove, even after the closure of the neural canal in the caudal region.

In embryos of stage G, which may be considered to belong to the close of this period, eighteen protovertebræ are present both in Pristiurus and Torpedo embryos.

The Alimentary Canal.

The alimentary canal at the commencement of this period (stage B) forms a space between the embryo and the yolk, ending blindly in front, but opening posteriorly by a widish

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[1] *Zeitschrift f. wiss. Zoologie*, 1873.

slit-like aperture, which corresponds to the anus of Rusconi (Pl. IV. fig. 7).

The cavity anteriorly has a more or less definite form, having lateral walls, as well as a roof and floor (Pl. V. fig. 10*b* and 10*c*). Posteriorly it is not nearly so definitely enclosed (Pl. V. fig. 10*a*). The ventral wall of the cavity is formed by yolk. But even in stage B there are beginnings of a cellular ventral wall derived from an ingrowth of cells from the two sides.

By stage C considerable progress has been made in the formation of the alimentary canal. Posteriorly it is as flattened and indefinite as during stage B (Pl. IX. figs. 2*b* and 2*c*). But in the anterior part of the embryo the cavity becomes much deeper and narrower, and a floor of cells begins to be formed for it (Pl. IX. fig. 2); and, finally, in front, it forms a definite space completely closed in on all sides by cells (Pl. IX. fig. 2*a*). Two distinct processes are concerned in effecting these changes in the condition of the alimentary cavity. One of these is a process of folding off the embryo from the blastoderm. The other is a simple growth of cells independent of any folding. To the first of these processes the depth and narrowness of the alimentary cavity is due; the second is concerned in forming its ventral wall. The combination of the two processes produces the peculiar triangular section which characterises the anterior closed end of the alimentary cavity at this stage. The process of the folding off of the embryo from the blastoderm resembles exactly the similar process in the embryo bird. The fold by which the constricting off of the embryo is effected is a perfectly continuous one, but may be conveniently spoken of as composed of a head-fold and two lateral folds.

Of far greater interest than the nature of these folds is the formation of the ventral wall of the alimentary canal. This, as has been said, is effected by a growth of cells from the two sides to the middle line (Pl. IX. fig. 2). The cells for this are however not derived from pre-existing hypoblast cells, but are formed spontaneously around nuclei of the yolk. This fact can be determined in a large number of sections, and is fairly well shewn in Pl. IX. fig. 2*na*. The cells are formed in the yolk, as has been already mentioned, by a simple aggregation of protoplasm around pre-existing nuclei.

The cells being described are in most cases formed close to the pre-existing hypoblast cells, but often require to undergo a considerable change of position before attaining their final situation in the wall of the alimentary canal.

I have already alluded to this feature in the formation of the ventral wall of the alimentary cavity. Its interest, as bearing on the homology of the yolk, is considerable, owing to the fact that the so-called yolk-cells of Amphibians play a similar part in supplying the ventral epithelium of the alimentary cavity, as do the cells derived from the yolk in Elasmobranchs.

The fact of this feature being common to the yolk-cells of Amphibians and the yolk of Elasmobranchs, supplies a strong argument in favour of the homology of the yolk-cells in the one case with the yolk in the other[1].

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[1] Nearly simultaneously with Chapter III. of the present monograph on the Development of Elasmobranchs, which dealt in a fairly complete manner with the genesis of cells outside the blastoderm, there appeared two important papers dealing with the same subject for Teleostei. One of these, by Professor Bambeke, Embryologie des Poissons Osseux, *Mém. Cour. Acad. Belgique*, 1875, which appeared some little time before my paper, and a second by Dr Klein, *Quart. Jour. of Micr. Sci.* April, 1876. In both of these papers a development of nuclei and of cells is described as occurring outside the blastoderm in a manner which accords fairly well with my own observations.

The conclusions of both these investigators differ however from my own. They regard the finely granular matter, in which the nuclei appear, as pertaining to the blastoderm, and morphologically quite distinct from the yolk. From their observations we can clearly recognize that the material in which the nuclei appear is far more sharply separated off from the yolk in Osseous Fish than in Elasmobranchs, and this sharp separation forms the main argument for the view of these authors. Dr Klein admits, however, that this granular matter (which he calls parablast) graduates in the typical food-yolk, though he explains this by supposing that the parablast takes up part of the yolk for the purpose of growth.

It is clear that the argument from a sharp separation of yolk and parablast cannot have much importance, when it is admitted (1) that in Osseous Fish there is a gradation between the two substances, while (2) in Elasmobranchs the one merges slowly and insensibly into the other.

The only other argument used by these authors is stated by Dr Klein in the following way. "The fact that the parablast has, at the outset, been forming one unit with what represents the archiblast, and, *while increasing has spread* i.e. *grown over the yolk* which underlies the segmentation-cavity, is, I think, the most absolute proof that the yolk is as much different from the parablast as it is from the archiblast." This argument to me merely demonstrates that certain of the nutritive elements of the yolk become in the course of development converted into protoplasm, a phenomenon which must necessarily be supposed to take place on my own as well as on Dr Klein's view of the nature of the yolk. My own views on the subject have already been fully stated. I regard the so-called yolk as composed of a larger or smaller amount of food-material imbedded

The history of the alimentary canal during the remainder of this period may be told briefly.

The folding off and closing of the alimentary canal in the anterior part of the body proceeds rapidly, and by stage D not only is a considerable tract of alimentary canal formed, but a great part of the head is completely folded off from the yolk (Pl. IX. fig. 3*a*). By stage F a still greater part is folded off. The posterior part of the alimentary canal retains for a long period its primitive condition. It is not until stage F that it begins to be folded off behind. After the folding has once commenced it proceeds with great rapidity, and before stage G, the hinder part of the alimentary canal becomes completely closed in.

The folding in of the gut is produced by two lateral folds, and the gut is not closed posteriorly.

It may be remembered that the neural canal also remained open behind. Thus both the neural and alimentary canals are open behind; and, since both of them extend to the posterior end of the body, they meet there, their walls coalesce, and a direct communication from the neural to the alimentary canal

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in protoplasm, and the meroblastic ovum as a body constituted of the same essential parts as a holoblastic ovum, though divided into regions which differ in the proportion of protoplasm they contain. I do not propose to repeat the positive arguments used by me in favour of this view, but content myself with alluding to the protoplasmic network found by Schultz and myself extending through the whole yolk, and to the similar network described by Bambeke as being present in the eggs of Osseous Fish after deposition but before impregnation. The existence of these networks is to me a conclusive proof of the correctness of my views. I admit that in Teleostei the 'parablast' contains more protoplasm than the homologous material in the Elasmobranch ovum, while it is probable that after impregnation the true yolk of Teleostei contains little or no protoplasm; but these facts do not appear to me to militate against my views.

I agree with Prof. Bambeke in regarding the cells derived from the subgerminal matter as homologous with the so-called yolk-cells of the Amphibian embryo.

I have recently, in some of the later stages of development, met with very peculiar nuclei of the yolk immediately beneath the blastoderm at some little distance from the embryo, Pl. IX. fig. 8. They were situated not in finely subgerminal matter, but amongst large yolk spherules. They were very large, and presented still more peculiar forms than those already described by me, being produced into numerous long filiform processes. The processes from the various nuclei were sometimes united together, forming a regular network of nuclei quite unlike anything that I have previously seen described.

The sub-germinal matter, in which the nuclei are usually formed, becomes during the later stages of development far richer in protoplasm than during the earlier. It continually arises at fresh points, and often attains to considerable dimensions, no doubt by feeding on yolk-spherules. Its development appears to be determined by the necessities of growth in the blastoderm or embryo.

is instituted. The process may be described in another way by saying that the medullary folds are continuous round the end of the tail with the lateral walls of the alimentary canal; so that, when the medullary folds unite to form a canal, this canal becomes continuous with the alimentary canal, which is closed in at the same time. In whatever way this arrangement is produced, the result of it is that it becomes possible to pass in a continuously closed passage along the neural canal round the end of the tail and into the alimentary canal. A longitudinal section shewing this feature is represented on Plate IX. fig. 7.

This communication between the neural and alimentary canals, which is coupled, as will be seen in the sequel, with the atrophy of a posterior segment of the alimentary canal, is a feature of great interest which ought to throw considerable light upon the meaning of the neural canal. So far as I know, no suggestion as to the origin of it has yet been made. It is by no means confined to Elasmobranchs, but is present in all the vertebrates whose embryos are situated at the centre and not at the periphery of the blastoderm. It has been described by Goette[1] in Amphibians and by Kowalevsky, Owsjannikow and Wagner[2] in the Sturgeon (Acipenser). The same arrangement is also stated by Kowalevsky[3] to exist in Osseous Fishes and Amphioxus. The same investigator has shewn that the alimentary and neural canals communicate in larval Ascidians, and we may feel almost sure that they do so in the Marsipobranchii.

The Reptilia, Aves, and Mammalia have usually been distinguished from other vertebrates by the possession of a well-developed allantois and amnion. I think that we may further say that the lower vertebrates, Pisces and Amphibia, are to be distinguished from the three above-mentioned groups of higher vertebrates, by the positive embryonic character that their neural and alimentary canals at first communicate pos-

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[1] *Entwicklungsgeschichte der Unke.*

[2] *Mélanges Biologiques de l'Académie Pétersbourg*, Tome VII.

[3] *Archiv f. mikros. Anat.* Vol. VII. p. 114. In the passage on this point Kowalevsky states that in Elasmobranchs the neural and alimentary canals communicate. This I believe to be the first notice published of this peculiar arrangement.

teriorly. The presence or absence of this arrangement depends on the different positions of the embryo in the blastoderm. In Reptiles, Birds and Mammals, the embryo occupies a central position in the blastoderm, and not, as in Pisces and Amphibia, a peripheral one at its edge. We can, in fact, only compare the blastoderm of the Bird and the Elasmobranch, by supposing that in the blastoderm of the Bird there has occurred an abbreviation of the processes, by which the embryo Elasmobranch is eventually placed in the centre of the blastoderm: as a result of this abbreviation the embryo Bird occupies *from the first a* central position in the blastoderm[1].

The peculiar relations of the blastoderm and embryo, and the resulting relations of the neural and alimentary canal, appear to me to be features of quite as great an importance for classification as the presence or absence of an amnion and allantois.

General features of the hypoblast.

There are but few points to be noticed with reference to the histology of the hypoblast cells. The cells of the dorsal wall of the alimentary cavity are columnar and form a single row. Those derived from the yolk to form the ventral wall are at first roundish, but subsequently assume a more columnar form.

The Notochord.

One of the most interesting features in the Elasmobranch development is the formation of the notochord from the hypo-

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[1] Vide Note on p. 68, also p. 81, and Pl. VIII. Fig. 1 and 2, and Comparison, &c., *Qy. Jour. of Micros. Sci.* July, 1875, p. 219. These passages give an account of the change of position of the Elasmobranch embryo, and the Note on p. 68 contains a speculation about the nature of the primitive streak with its contained primitive groove. I have suggested that the primitive streak is probably to be regarded as a rudiment at the position where the edges of the blastoderm coalesced to give to the embryos of Birds and Mammals the central position which they occupy.

If my hypothesis should turn out to be correct, various, now unintelligible, features about the primitive streak would be explained: such as its position behind the embryo, the fusion of the epiblast and mesoblast in it, the groove it contains, &c.

The possibility of the primitive streak representing the blastopore, as it in fact does according to my hypothesis, ought also to throw light on E. Van Beneden's recent researches on the development of the Mammalian ovum.

In order clearly to understand the view here expressed, the reader ought to refer to the passages above quoted.

blast. All the steps in the process by which this takes place can be followed with great ease and certainty.

Up to stage B the hypoblast is in contact with the epiblast immediately below the medullary groove, but exhibits no trace of a thickening or any other formation at that point.

Between stage B and C the notochord first arises.

In the hindermost sections of this stage the hypoblast retains a perfectly normal structure and uniform thickness throughout. In next few sections, Pl. IX. fig. 1 *c*, *ch'*, a slight thickening is to be observed in the hypoblast, immediately below the medullary canal. The layer, which elsewhere is composed of a single row of cells, here becomes two cells deep, but no sign of a division into two layers exhibited.

In the next few sections the thickening of the hypoblast becomes much more pronounced; we have, in fact, a ridge projecting from the hypoblast towards the epiblast (Pl. IX. fig. 1 *b*, *ch'*).

This ridge is pressed firmly against the epiblast, and causes in it a slight indentation. The hypoblast in the region of the ridge is formed of two layers of cells, the ridge being entirely due to the uppermost of the two.

In sections in front of this a cylindrical rod, which can at once be recognised as the notochord and is continuous with the ridge just described, begins to be split off from the hypoblast. It is difficult to say at what point the separation of this rod from the hypoblast is completed, since all intermediate gradations between complete separation and complete attachment are to be seen.

Where the separation first appears, a fairly thick bridge of hypoblast is left connecting the two lateral halves of the layer, but anteriorly this bridge becomes excessively delicate and thin (Pl. IX. fig. 1 *c*), and in some cases is barely visible except with high powers.

From the series of sections represented, it is clear that the notochord commences to be separated from the hypoblast anteriorly, and that the separation gradually extends backwards.

The posterior extremity of the notochord remains for a long time attached to the hypoblast; and it is not till the end of the period treated of in this chapter that it becomes completely free.

A sheath is formed around the notochord, very soon after its formation, at a stage intermediate between stages C and D. This sheath is very delicate, though it stains with both osmic acid and hæmatoxylin. I conclude from its subsequent history, that it is to be regarded as a product of the cells of the notochord, but at the same time it should be stated that it precisely resembles membrane-like structures, which I have already described as being probably artificial.

Towards the end of this period the cells of the notochord become very much flattened vertically, and cause the well-known stratified appearance which characterises the notochord in longitudinal sections. In transverse sections the outlines of the cells of the notochord appear rounded.

Throughout this period the notochord cells are filled with yolk spherules, and near its close small vacuoles make their appearance in them.

An account of the development of the notochord, substantially similar to that I have just given, appeared in my preliminary paper[1] on the development of the Elasmobranch fishes.

To the remarks which were there made, I have little to add. There are two possible views, which can be held with reference to the development of the notochord from the hypoblast.

We may suppose that this is the primitive mode of development of the notochord, or we may suppose that the separation of the notochord from the hypoblast is due to a secondary process.

If the latter view is accepted, it will be necessary to maintain that the mesoblast becomes separated from the hypoblast as three separate masses, two lateral, and one median, and that the latter become separated much later than the two former.

We have, I think, no right to assume the truth of this view without further proof. The general admission of assumptions of this kind is apt to lead to an injurious form of speculation, in which every fact presenting a difficulty in the way of some general theory is explained away by an arbitrary assumption, while all the facts in favour of it are taken for granted. It is however clear that no theory can ever be fairly tested so long as logic of this kind is permitted. If, in the present instance,

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[1] *Loc. cit.*

the view is adopted that the notochord has in reality a mesoblastic origin, it will be possible to apply the same view to every other organ derived from the hypoblast, and to say that it is really mesoblastic, but has become separated at rather a late period from the hypoblast.

If, however, we provisionally reject this explanation, and accept the other alternative, that the notochord is derived from the hypoblast, we must be prepared to adopt one of two views with reference to the development of the notochord in other vertebrates. We must either suppose that the current statements as to the development of the notochord in other vertebrates are inaccurate, or that the notochord has only become secondarily mesoblastic.

The second of these alternatives is open to the same objections as the view that the notochord has only apparently a hypoblastic source in Elasmobranchs, and, provisionally at least, the first of them ought to be accepted. The reasons for accepting this alternative fall under two heads. In the first place, the existing accounts and figures of the development of the notochord exhibit in almost all cases a deficiency of clearness and precision. The exact stage necessary to complete the series never appears. It cannot, therefore, at present be said that the existing observations on the development of the notochord afford a strong presumption against its hypoblastic origin.

In the second place, the remarkable investigations of Hensen[1], on the development of the notochord in Mammalia, render it very probable that, in this group, the notochord is developed from the hypoblast.

Hensen finds that in Mammalia, as in Elasmobranchs, the mesoblast forms two independent lateral masses, one on each side of the medullary canal.

After the commencing formation of the protovertebræ the hypoblast becomes considerably thickened beneath the medullary groove; and, though he has not followed out all the steps of the process by which this thickening is converted into the notochord, yet his observations go very far towards proving that it does become the notochord.

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[1] *Zeitschrift f. Anat. u. Entwicklungsgeschichte*, Vol. I. p. 366.

[2] *Sitz. der Gesell. zu Marburg*, Jan. 1876.

Against the observations of Hensen, there ought, however, to be mentioned those of Lieberkühn[2]. He believes that the two lateral masses of mesoblast, described by Hensen (in an earlier paper than the one quoted), are in reality united by a delicate layer of cells, and that the notochord is formed from a thickening of these.

Lieberkühn gives no further statements or figures, and it is clear that, even if there is present the delicate layer of mesoblast, which he fancies he has detected, yet this cannot in any way invalidate such a section as that represented on Pl. x. fig. 40, of Hensen's paper.

In this figure of Hensen's, the hypoblast cells become distinctly more columnar, and the whole layer much thicker immediately below the medullary canal than elsewhere, and this independently of any possible layer of mesoblast.

It appears to me reasonable to conclude that Lieberkühn's statements do not seriously weaken the certainty of Hensen's results.

In addition to the observations of Hensen's on Mammalia, those of Kowalevsky and Kuppfer on Ascidians may fairly be pointed to as favouring the hypoblastic origin of the notochord.

It is not too much to say that at the present moment the balance of evidence is in favour of regarding the notochord as a hypoblastic organ.

This conclusion is, no doubt, rather startling, and difficult to understand. The only feature of the notochord in its favour is the fact of its being unsegmented[1].

Should it eventually turn out that the notochord is developed in most vertebrates from the mesoblast, and only exceptionally from the hypoblast, the further question will have to be settled as to whether it is primitively a hypoblastic or a mesoblastic organ; but, from whatever layer it has its source, an excellent example will be afforded of an organ changing from the layer in which it was originally developed into another distinct layer.

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[1] In my earlier paper I suggested that the endostyle of Ascidians afforded an instance of a supporting organ being derived from the hypoblast. This parallel does not hold since the endostyle has been shewn to possess a secretory function. I never intended (as has been imagined by Professor Todaro) to regard the endostyle as the homologue of the notochord.

CHAPTER VI.

DEVELOPMENT OF THE TRUNK DURING STAGES G TO K.

BY the stage when the external gills have become conspicuous objects, the rudiments of the greater number of the important organs of the body are definitely established.

Owing to this fact the first appearance of the external gills forms a very convenient break in the Elasmobranch development; and in the present chapter the history is carried on to the period of this occurrence.

While the last chapter dealt for the most part with the formation of the main organic systems from the three embryonic layers, the present one has for its subject the gradual differentiation of these systems into individual organs. In treating of the development of the separate organs a divergence from the plan of the last chapter becomes necessary, and the following arrangement has been substituted for it. First of all an account is given of the development of the external epiblast, which is followed by a description of the organs derived from the mesoblast and of the notochord.

External Epiblast.

During stages G to I the epiblast[1] is formed of a single layer of flattened cells; and in this, as in the earlier stages, it deserves to be especially noticed that the epiblast is never more than *one cell deep*, and is therefore incapable of presenting any differentiation into nervous and epidermic layers. (Pl. x. fig. 1—5).

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[1] Unless the contrary is stated, the facts recorded in this chapter apply only to the genera Scyllium and Pristiurus.

The cells which compose it are flattened and polygonal in outline, but more or less spindle-shaped in section. They present a strong contrast to the remaining embryonic cells of the body in possessing a considerable quantity of clear protoplasm, which in most other cells is almost entirely absent. Their granular nucleus is rounded or oval, and typically contains a single nucleolus. Frequently, however, two nucleoli are present, and when this is the case an area free from granules is to be seen around each nucleolus, and a dark line, which could probably be resolved into granules by the use of a sufficiently high magnifying power, divides the nucleus into two halves. These appearances probably indicate that nuclei, in which two nucleoli are present, are about to divide.

The epiblast cells vary in diameter from ·022 to ·026 Mm. and their nuclei from ·014 to ·018 Mm. They present a fairly uniform character over the greater part of the body. In Torpedo they present nearly the same characters as in Pristiurus and Scyllium, but are somewhat more columnar. (Pl. x. fig. 7.)

Along the summit of the back from the end of the tail to the level of the anus, or slightly beyond this, epiblast cells form a fold—the rudiment of the embryonically undivided dorsal fin—and the cells forming this, unlike the general epiblast cells, are markedly columnar; they nevertheless, here as elsewhere, form but a single layer. (Pl. x. fig. 3 and 5 *df.*) Although at this stage the dorsal fin is not continued as a fold anteriorly to the level of the anus, yet a columnar thickening or ridge of epiblast, extending along the median dorsal line nearly to the level of the heart, forms a true morphological prolongation of the fin.

On the ventral side of the tail is present a rudiment of the ventral unpaired fin, which stops short of the level of the anus, but, though less prominent, is otherwise quite similar to the dorsal fin and continuous with it round the end of the tail. At this stage the mesoblast has no share in forming either fin.

In many sections of the tail there may be seen on each side two folds of skin, which are very regular, and strongly simulate the rudimentary fins just described. The cells composing them are, however, not columnar, and the folds themselves are merely artificial products due to shrinking.

At a stage slightly younger than K an important change takes place in the epiblast.

From being composed of a single layer of cells it becomes two cells deep. The two layers appear first of all anteriorly, and subsequently in the remaining parts of the body. At first, both layers are formed of flattened cells (Pl. X. fig. 8, and XI. fig. 9); but at a stage slightly subsequent to that dealt with in the present chapter, the cells of the inner of the two layers become columnar, and thus are established the two strata always present in the epidermis of adult vertebrates, viz. an outer layer of flattened cells and an inner one of columnar cells[1].

The history of the epiblast in Elasmobranchs is interesting, from the light which it throws upon the meaning of the nervous and epidermic layers into which the epiblast of Amphibians and some other Vertebrates is divided. The Amphibians and Elasmobranchs present the strongest contrast in the development of their epiblast, and it is worth while shortly to review and compare the history of the layer in the two groups.

In Amphibians the epiblast is from the first divided into an outer stratum formed of a single row of flattened cells, and an inner stratum composed of several rows of more rounded cells. These two strata were called by Stricker the nervous and epidermic layers, and these names have been very generally adopted.

Both strata have a share in forming the general epiblast, and though eventually they partially fuse together, there can be but little doubt that the horny layer of the adult epiblast, where such can be distinguished[2], is derived from the epidermic layer of the embryo, and the mucous layer of the epiblast from the embryonic nervous layer. Both layers of the epiblast assist in the formation of the cerebro-spinal nervous system, and there also at first fuse together[3], though the epidermic layer probably separates itself again, as the central epithelium of the spinal canal. The lens and auditory sac are derived exclusively from

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[1] The layers are known as epidermic (horny) and mucous layers by English writers, and as Hornschicht and Schleimschicht by the Germans. For their existence in all Vertebrates, vide Leydig *Ueber allgemeine Bedeckungen der Amphibien*, p. 20. Bonn, 1876.

[2] Vide Leydig *loc. cit.*

[3] Vide Götte *Entwicklungsgeschichte der Unke.*

the nervous layer of the epidermis, while this layer also has the greater share in forming the olfactory sac.

In Elasmobranchs the epiblast is at first uniformly composed of a single row of cells. The part of the layer which will form the central nervous system next becomes two or three cells deep, but presents no distinction into two layers; the remaining portions of the layer remain, as before, one cell deep. Although the epiblast at first presents this simple structure, it eventually, as we have seen, becomes divided throughout into two layers, homologous with the two layers which arise so early in Amphibians. The outer one of the two forms the horny layer of the epidermis and the central epithelium of the neural canal. The inner one, the mucous layer of the epidermis and the nervous part of the brain and spinal cord. Both layers apparently enter into the formation of the organs of sense.

While there is no great difficulty in determining the equivalent parts of the epidermis in Elasmobranchs and Amphibians, it still remains an open question in which of these groups the epiblast retains its primitive condition.

Though it is not easy to bring conclusive proofs on the one side or the other, the balance of argument appears to me to be decidedly in favour of regarding the condition of the epiblast in Elasmobranchs, and most other Vertebrates, as the primitive one, and its condition in Amphibians as a secondary one, due to the throwing back of the differentiation of their epiblast into two layers to a very early period in their development.

In favour of this view are the following points: (1) That a *primitive* division of the epiblast into two layers is unknown in the animal kingdom, except amongst Amphibians and (?) Osseous Fish. (2) That it appears more likely for a particular feature of development to be thrown back to an earlier period, than for such an important feature as a distinction between two primary layers to be absolutely lost during an early period of development, and then to re-appear again in later stages.

The fact of the epiblast of the neural canal being divided, like the remainder of the layer, into nervous and epidermic parts, cannot, I think, be used as an argument in favour of the opposite view to that here maintained.

It seems probable that the central canal of the nervous system arose as an involution from the exterior, and therefore that the epidermis lining it is in reality merely a part of the external epidermis, and as such is naturally separated from the true nervous structures adjacent to it[1].

Leaving the general features of the external skin, I pass to the special organs derived from it during the stage just anterior to K.

The unpaired Fins. The unpaired fins have grown considerably, and the epiblast composing them becomes, like the remainder of the layer, divided into two strata, both however composed of more or less columnar cells. The ventral fin has now become more prominent than the dorsal fin; but the latter extends forward as a fold quite to the anterior part of the body.

The paired Fins. Along each side of the body there appears during this stage a thickened line of epiblast, which from the first exhibits two special developments: one of these just in front of the anus, and a second and better marked one opposite the front end of the segmental duct. These two special thickenings are the rudiments of the paired fins, which thus arise as special developments of a continuous ridge on each side, precisely like the ridges of epiblast which form the rudiments of the unpaired fins.

Similar thickenings to those in Elasmobranchs are found at the ends of the limbs in the embryos of both Birds and Mammals, in the form of caps of columnar epiblast[2].

The ridge, of which the limbs are special developments, is situated on a level slightly ventral to that of the dorsal aorta, and extends from just behind the head to the level of the anus. It is not noticeable in surface views, but appears in sections as a portion of the epiblast where the cells are more columnar than elsewhere; precisely resembling in this respect the forward continuation of the dorsal fin. At the present stage the posterior thickenings of this ridge which forms the abdominal fins are so slight as to be barely visible, and their real nature can only be detected by a careful comparison between sections

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[1] Vide Self, *Development of Spinal Nerves in Elasmobranchs.* Phil. Transact. 1876.

[2] For Birds, vide *Elements of Embryology*, Foster and Balfour, pp. 144—145, and for Mammals, Kölliker *Entwicklungsgeschichte*, p. 283.

of this and the succeeding stages. The rudiments of the anterior pair of limbs are more visible than those of the posterior, though the passage between them and the remainder of the ridges is most gradual. Thus at first the rudiments of both the limbs are nothing more than slight thickenings of the epiblast, where its cells are more columnar than elsewhere. During stage K the rudiments of both pairs of limbs, but especially of the anterior pair, grow considerably, while at the same time the thickened ridge of epiblast which connects them together rapidly disappears. The thoracic limbs develope into an elongated projecting fold of epiblast, in every way like the folds forming the unpaired fins; while at the same time the cells of the subjacent mesoblast become closely packed, and form a slight projection, at the summit of which the fold of the epiblast is situated (Pl. XI. fig. 9). The maximum projection of the thoracic fin is slightly in advance of the front end of the segmental duct. The abdominal fins do not, during stage K, develope quite so fast as the thoracic, and at its close are merely elongated areas where the epiblast is much thickened, and below which the mesoblast is slightly condensed. In the succeeding stages they develope into projecting folds of skin, precisely as do the thoracic fins.

The features of the development of the limbs just described, are especially well shewn in Torpedo; in the embryos of which the passage from the general linear thickening of epiblast into the but slightly better marked thickening of the thoracic fin is very gradual, and the fact of the limb being nothing else than a special development of the linear lateral thickening is proved in a most conclusive manner.

If the account just given of the development of the limbs is an accurate record of what really takes place, it is not possible to deny that some light is thrown by it upon the first origin of the vertebrate limbs. The facts can only bear one interpretation, *viz.: that the limbs are the remnants of continuous lateral fins.*

The unpaired dorsal fin develops as a continuous thickening, which then grows up into a projecting fold of columnar cells. The greater part of this eventually atrophies, but three separate lobes are left which form the two dorsal fins and the upper lobe of the caudal fin.

The development of the limbs is almost identically similar to that of the dorsal fins. There appears a lateral linear thickening of epiblast, which however does not, like the similar thickening of the fins, grow into a distinct fold. Its development becomes confined to two special points, at each of which is formed a continuous elongated fold of columnar cells precisely like the fold of skin forming the dorsal fins. These two folds form the paired pins. If it be taken into consideration that the continuous lateral fin, of which the rudiment appears in Elasmobranchs, does not exist in any adult Vertebrate, and also that a continuous dorsal fin exists in many Fishes, the small differences in development between the paired fin and the dorsal fins will be seen to be exactly those which might have been anticipated beforehand. Whereas the continuous dorsal fin, which often persists in adult fishes, attains a considerable development before vanishing, the originally continuous lateral one has only a very ephemeral existence.

While the facts of development strongly favour a view which would regard the limbs as remnants of a primitively continuous lateral fin, there is nothing in the structure of the limbs of adult Fishes which is opposed to this view. Externally they closely resemble the unpaired fins, and both their position and nervous supply appear clearly to indicate that they do not belong to one special segment of the body. They appear rather to be connected with a varying number of segments; a fact which would receive a simple explanation on the hypothesis here adopted[1].

My researches throw no light on the nature of the skeletal parts of the limb, but the suggestion which has been made by Günther[2] with reference to the limb of Ceratodus (the most primitive known), that it is a modification of a series of parallel rays, would very well suit the view here proposed.

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[1] For the nervous supply in fishes, vide Stannius *Peripher. Nerv. System d. Fische.* In Osseous Fishes he states that the thoracic fin is supplied by branches from the first three though sometimes from the first four spinal nerves. In Accipenser there are branches from the first six nerves. In Spinax the limb is supplied by the rami anteriores of the fourth and succeeding ten spinal nerves. In the Rays not only do the sixteen anterior spinal nerves unite to supply the fin, but in all there are rami anteriores from thirty spinal nerves which pass to the thoracic limb.

[2] *Philosophical Transactions*, 1871.

Dr Dohrn[1] in speaking of the limbs, points out the difficulties in the way of supposing that they can have originated *de novo*, and not by the modification of some preexisting organ, and suggests that the limbs are modified gill-arches; a view similar to which has been hinted at by Professor Gegenbaur[2].

Dr Dohrn has not as yet given the grounds for his determination, so that any judgment on his views is premature.

None of my observations on Elasmobranchs lends any support to these views; but perhaps, while regarding the limbs as the remains of a continuous fin, it might be permissible to suppose that the pelvic and thoracic girdles are altered remnants of the skeletal parts of some of the gill-arches which have vanished in existing Vertebrates.

The absence of limbs in the Marsipobranchii and Amphioxus, for reasons already insisted upon by Dr Dohrn[3], cannot be used as an argument against limbs having existed in still more primitive Vertebrates.

Though it does not seem probable that a dorsal and ventral fin can have existed contemporaneously with lateral fins (at least not as continuous fins), yet, judging from such forms as the Rays, there is no reason why small balancing dorsal and caudal fins should not have coexisted with fully developed lateral fins.

Mesoblast. G—K.

The mesoblast in Stage F forms two independent lateral plates, each with a splanchnic and somatic layer, and divided, as before explained, into a vertebral portion and a parietal portion. At their peripheral edge these plates are continuous with the general mesoblastic tissue of the non-embryonic part of the blastoderm; except in the free parts of the embryo, where they are necessarily separated from the mesoblast of the yolk-sac, and form completely independent lateral masses of cells.

During the stages G and H, the two layers of which the mesoblast is composed cease to be in contact, and leave be-

[1] *Ursprung d. Wirbelthiere und Functionswechsels.*

[2] *Grundriss d. Vergleichenden Anat.* p. 494.

[3] *Loc. cit.*

tween them a space which constitutes the commencement of the body-cavity (Pl. X. fig. 1). From the very first this cavity is more or less clearly divided into two distinct parts; one of them in the vertebral portion of the plates of mesoblast, the other in the parietal. The cavity in the parietal part of the plates alone becomes the true body-cavity. It extends uninterruptedly through the anterior parts of the embryo, but does not appear in the caudal region, being there indicated only by the presence of two layers in the mesoblast plates. Though fairly wide below, it narrows dorsally before becoming continuous with the cavity in the vertebral plates. The line of junction of the vertebral and parietal plates is a little ventral to the dorsal summit of the alimentary canal (Pl. X. fig. 5). Owing to the fact that the vertebral plates are split up into a series of segments (protovertebræ), the section of the body-cavity they enclose is necessarily also divided into a series of segments, one for each protovertebra.

Thus the whole body-cavity consists of a continuous parietal space which communicates by a series of apertures with a number of separate cavities enclosed in the protovertebræ. The cavity in each of the protovertebræ is formed of a narrowed dorsal and a dilated ventral segment, the latter on the level of the dorsal aorta (Pl. X. fig. 5). Cavities are present in all the vertebral plates with the exception of a few far back in the tail; and exist in part of the caudal region posterior to that in which a cavity in the parietal plate is present.

Protovertebræ. Each protovertebra[1] or vertebral segment of the mesoblast plate forms a flattened rectangular body, ventrally continuous with the parietal plate of mesoblast. During stage G the dorsal edge of the protovertebræ is throughout on about a level with the ventral third of the spinal cord. Each vertebral plate is composed of two layers, a somatic and a splanchnic, and encloses the already-mentioned section of the body cavity. The cells of both layers of the plate are columnar, and each consists of a very large nucleus, invested by a delicate layer of protoplasm.

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[1] No attempt has been made to describe in detail the different appearances presented by the protovertebræ in the various parts of the body, but in each stage a protovertebra from the dorsal region is taken as typical.

Before the end of stage H the inner or splanchnic wall of the protovertebra loses its simple constitution, owing to the middle part of it, opposite the dorsal two-thirds of the notochord, undergoing peculiar changes. These changes are indicated in transverse sections (Pl. x. fig. 5 and 6 *m p'*), by the cells in the part we are speaking of acquiring a peculiar angular appearance, and becoming one or two deep; and the meaning of the changes is at once shewn by longitudinal horizontal sections. These prove (Pl. xi. fig. 10) that the cells in this situation have become elongated in a longitudinal direction, and, in fact, form typical spindle-shaped embryonic muscle-cells, each with a large nucleus. Every muscle-cell extends for the whole length of a protovertebra, and in the present stage, or at any rate in stage I, acquires a peculiar granulation, which clearly foreshadows transverse striation (Pl. xi. fig. 11—13).

Thus by stage H a small portion of the splanchnopleure which forms the inner layer of each protovertebra, becomes differentiated into a distinct band of longitudinal striated muscles; these almost at once become functional, and produce the peculiar serpentine movements of the embryo, spoken of in a previous chapter, p. 76.

It may be well to say at once that these muscles form but a very small part of the muscles which eventually appear; which latter are developed at a very much later period from the remaining cells of the protovertebræ. The band developed at this stage appears to be a special formation, which has arisen through the action of natural selection, to enable the embryo to meet its respiratory requirements, by continually moving about, and so subjecting its body to fresh oxydizing influences; and as such affords an interesting example of an important structure acquired during and for embryonic life.

Though the cavities in the protovertebræ are at first perfectly continuous with the general body-cavity, of which indeed they merely form a specialized part, yet by the close of stage H they begin to be constricted off from the general body-cavity, and this process is continued rapidly, and completed shortly after stage I, and considerably before the commencement of stage K. (Pl. x. fig. 6 and 8). While this is taking place, part of the splanchnic layer of each protovertebra, immediately below the muscle-band just described, begins to proliferate, and produce a number of cells, which at once grow in between the muscles and the notochord. These cells are very easily seen both in transverse and longitudinal sections, and form the commencing vertebral bodies (Pl. x. fig. 6, and Pl. xi. fig. 10 and 11 *Vr*).

At first the vertebral bodies have the same segmentation as the protovertebræ from which they sprang; that is to say, they form masses of embryonic cells separated from each other by narrow slits, continuous with the slits separating the protovertebræ. They have therefore at their first appearance a segmentation completely different from that which they eventually acquire (Pl. xi. fig. 11).

After the separation of the vertebral bodies from the protovertebræ, the remaining parts of the protovertebræ may be called muscle-plates; since they become directly converted into the whole voluntary muscular system of the trunk. At the time when the cavity of the muscle-plates has become completely separate from the body-cavity, the muscle-plates themselves are oblong structures, with two walls enclosing the cavity just mentioned, in which the original ventral dilatation is still visible. The outer or somatic wall of the plates retains its previous simple constitution. The splanchnic wall has however a somewhat complicated structure. It is composed dorsally and ventrally of a columnar epithelium, but in its middle portion of the muscle-cells previously spoken of. Between these and the central cavity of the plates the epithelium forming the remainder of the layer commences to insert itself; so that between the first-formed muscle and the cavity of the muscle-plate there appears a thin layer of cells, not however continuous throughout.

At the end of the period *K* the muscle-plates have extended dorsally two-thirds of the way up the sides of the spinal cord, and ventrally to the level of the segmental duct. Their edges are not straight, but are bent into an angular form, with the apex pointing forwards. Vide Pl. xi. fig. 17 *mp*.

Before the end of the period a number of connective-tissue cells make their appearance, and extend upwards from the dorsal summit of the muscle-plates around the top of the spinal cord. These cells are at first rounded, but become typical branched connective-tissue cells before the close of the period (Pl. x. fig. 7 and 8).

Between stages I and K the bodies of the vertebræ rapidly increase in size and send prolongations downwards and inwards to meet below the notochord.

These soon become indistinguishably fused with other cells which appear in the area between the alimentary cavity and the notochord, but probably serve alone to form the vertebral bodies, while the cells adjoining them form the basis for the connective tissue of the kidneys, &c.

The vertebral bodies also send prolongations dorsalwards between the sides of the spinal cord and the muscle-plates. These grow round till they meet above the spinal and enclose the dorsal nerve-roots. They soon however become fused with the dorsal prolongations from the muscle-plates, at least so far as my methods of investigation enable me to determine; but it appears to me probable that they in reality remain distinct, and become converted into the neural arches, while the connective-tissue cells from the muscle-plates form the adjoining subcutaneous and inter-muscular connective tissue.

All the cells of vertebral rudiments become stellate and form typical embryonic connective tissue. The rudiments however still retain their primitive segmentation, corresponding with that of the muscle-plates, and do not during this period acquire their secondary segmentation. Their segmentation is however less clear than it was at an earlier period, and in the dorsal part of the vertebral rudiments is mainly indicated by the dorsal nerve-roots, which always pass out in the interval between two vertebral rudiments. Vide Pl. XI. fig. 12 *pr.*

Intermediate Cell-Mass. At about the period when the muscle-plates become completely free, a fusion takes place between the somatopleure and splanchnopleure immediately above the dorsal extremity of the true body-cavity (Pl. x. fig. 6). The cells in the immediate neighbourhood of this fusion form a special mass, which we may call the intermediate cell-mass—a name originally used by Waldeyer for the homologous cells in the Chick. Out of it are developed the urino-genital organs and the adjoining tissues. At first it forms little more than a columnar epithelium, but by the close of the period is divided into (1) An epithelium on the free surface; from this are derived the glandular parts of the kidneys and functional parts of the genital glands; and (2) a subjacent stroma which forms the basis for the connective tissue and vascular parts of these organs.

To the history of these parts a special section is devoted; and I now pass to the description of the mesoblast which lines the body-cavity and forms the connective tissue of the body-wall, and the muscular and connective tissue of the wall of the alimentary canal.

Body-Cavity and parietal plates. By the close of stage H, as has been already mentioned, a cavity is formed between the somatopleure and splanchnopleure in the anterior part of the trunk, which rapidly widens during the succeeding stages. Anteriorly, it invests the heart, which arises during stage G, as a simple space between the ventral wall of the throat and the splanchnopleure (Pl. x. fig. 4). Posteriorly it ends blindly.

This cavity forms in the region of the heart the rudiment of the pericardial cavity. The remainder of the cavity forms the true body-cavity.

Immediately behind the heart the alimentary canal is still open to the yolk-sac, and here naturally the two lateral halves of the body-cavity are separated from each other. In the tail of the embryo no body-cavity has appeared by stage I, although the parietal plates of mesoblast are distinctly divided into somatic and splanchnic layers. In the caudal region the lateral plates of mesoblast of the two sides do not unite ventrally, but are, on the contrary, quite disconnected. Their ventral edge is moreover much swollen (Pl. x. fig. 1). At the caudal swelling the mesoblast plates cease to be distinctly divided into somatopleure and splanchnopleure, and more or less fuse with the hypoblast of the caudal vesicle (Pl. x. fig. 2).

Between stages I and K the body-cavity extends backwards behind the point where the anus is about to appear, though it never reaches quite to the extreme end of the tail. The backward extension of the body-cavity, as is primitively the case everywhere, is formed of two independent lateral halves (Pl. xi. fig. 9 *a*). Anteriorly, opposite the hind end of the small intestine, these two lateral halves unite ventrally to form a single cavity in which hangs the small intestine (Pl. x. fig. 8) suspended by a very short mesentery.

The most important change which takes place in the body-cavity during this period is the formation of a septum which separates off a pericardial cavity from the true body-cavity.

Immediately in front of the liver the splanchnic and somatic walls of the body come into very close contact, and I believe unite over the greater part of their extent. The septum so formed divides the original body-cavity into an anterior section or pericardial cavity, and a posterior section or true body-cavity. There is left, however, on each side dorsally a rather narrow passage which serves to unite the pericardial cavity in front with the true body-cavity behind.

In Pl. x. fig. 8 *a*, there is seen on one side a section through this passage, while on the other side the passage is seen to be connected with the pericardial cavity.

It is not possible from transverse sections to determine for certain whether the septum spoken of is complete. An examination of longitudinal horizontal sections from an embryo belonging to the close of the stage K has however satisfied me that this septum, by that stage at any rate, is fully formed.

The two lateral passages spoken of above probably unite in the adult to form the passage connecting the pericardial with the peritoneal cavity, which, though provided with but a single orifice into the pericardial cavity, divides into two limbs before opening into the peritoneal cavity.

The body-cavity undergoes no further changes of importance till the close of the period.

Somatopleure and Splanchnopleure. Both the somatic and splanchnic walls of the body-cavity during stage I exhibit a simple uniform character throughout their whole extent. They are formed of columnar cells where they line the dorsal part of the body-cavity, but ventrally of more rounded and irregular cells (Pl. x. fig. 5).

In them may occasionally be seen aggregations of very peculiar and large cells with numerous highly refracting spherules; the cells forming these are not unlike the *primitive ova* to be described subsequently, but are probably large cells derived from the yolk.

It is during the stage intermediate between I and K that the first changes become visible which indicate a distinction between an epithelium (endothelium) lining the body-cavity and the connective tissue adjoining this.

There are at first but very few connective-tissue cells between the epithelium of the somatic layer of the mesoblast and the epiblast, but a connection between them is established by peculiar protoplasmic processes which pass from the one to the other (Pl. X. fig. 8). Towards the end of stage K, however, there appears between the two a network of mesoblastic cells connecting them together. In the rudimentary outgrowth to form the limbs the mesoblast cells of the somatic layer are crowded in an especially dense manner.

From the first the connective-tissue cells around the hypoblastic epithelium of the alimentary tract are fairly numerous (Pl. X. fig. 8), and by the close of this period become concentrically arranged round the intestinal epithelium, though not divided into distinct layers. A special aggregation of them is present in the hollow of the rudimentary spiral valve.

Behind the anal region the two layers of the mesoblast (somatic and splanchnic) completely fuse during stage K, and form a mass of stellate cells in which no distinction into two layers can be detected (Pl. XI. fig. 9 *c*, 9 *d*).

The alimentary canal, which at first lies close below the aorta, becomes during this period gradually carried further and further from this, remaining however attached to the roof of the body-cavity by a thin layer of the mesoblast of the splanchnopleure formed of an epithelium on each side, and a few interposed connective-tissue cells. This is the mesentery which by the close of stage K is of considerable length in the region of the stomach, though shorter elsewhere.

The above account of the protovertebræ and body-cavity applies solely to the genera Pristiurus and Scyllium. The changes of these parts in Torpedo only differ from those of Pristiurus in unimportant though fairly noticeable details. Without entering into any full description of these it may be pointed out that both the true body-cavity and its continuations into the protovertebræ appear later in Torpedo than in Pristiurus and Scyllium. In some cases even the muscle-plates become definitely separated and independent before the true body-cavity has appeared. As a result of this the primitive continuity of the body-cavity and cavity of the muscle-plates becomes to a certain extent masked, though its presence may easily be detected by the obvious continuity which at first exists between the somatic and splanchnic layers of mesoblast and the two layers of the muscle-plate. In the muscle-plate itself the chief point to be noticed is the fact that the earlier formed bands of muscles (*mp'*) arise very much later, and are less conspicuous, in Torpedo than in the genera first described. They are however present and functional.

The anatomical relations of the body-cavity itself are precisely the same in Torpedo as in Pristiurus and Scyllium, and the pericardial cavity becomes separated from the peritoneal in same way in all the genera; the two lateral canals connecting the two cavities being also present in all the three genera. The two independent parietal plates of mesoblast of the posterior parts of the body have ventrally a swollen edge, as in Pristiurus, and in this a cavity appears which forms a posterior continuation of the true body-cavity.

Resumé. The primitive independent mesoblast plates of the two sides of the body become divided into two layers, a somatic and a splanchnic (Hautfaserblatt and Darmfaserblatt). At the same time in the dorsal part of the mesoblast plate a series of transverse splits appear which mark out the limits of the protovertebræ and serve to distinguish a dorsal or vertebral part of the plate from a ventral or parietal part.

Between the somatic and splanchnic layers of the mesoblast plate a cavity arises which is continued quite to the summit of the vertebral part of the plate. This is the primitive body-cavity; and at first the cavity is divided into two lateral and independent halves.

The next change which takes place is the complete separation of the vertebral portion of the plate from the parietal; thereby the upper segmented part of the body-cavity becomes isolated and separated from the lower and unsegmented part. In connection with this change in the constitution of the body-cavity there are formed a series of rectangular plates, each composed of two layers, a somatic and a splanchnic, between which is the cavity originally continuous with the body-cavity. The splanchnic layer of the plates buds off cells to form the rudiments of the vertebral bodies which are originally segmented in the same planes as the protovertebræ. The plates themselves remain as the muscle-plates and develop a special layer of muscle (*m p′*) in their splanchnic layer.

In the meantime the parietal plates of the two sides unite ventrally throughout the intestinal and cardiac regions of the body, and the two primitively isolated cavities contained in them coalesce. Posteriorly however the plates do not unite ventrally, and their contained cavities remain distinct.

At first the pericardial cavity is quite continuous with the body-cavity; but by the close of the period included in the present chapter it becomes separated from the body-cavity by a septum in front of the liver, which is however pierced dorsally by two narrow channels.

The parts derived from the two layers of the mesoblast (not including special organs or the vascular system) are as follow:—

From the somatic layer are formed

(1) A considerable part of the voluntary muscular system of the body.
(2) The dermis.
(3) A large part of the intermuscular connective tissue.
(4) Part of the peritoneal epithelium.

From the splanchnic layer are formed

(1) A great part of the voluntary muscular system.
(2) Part of the intermuscular connective tissue (?).
(3) The axial skeleton.
(4) The muscular and connective-tissue wall of the alimentary tract.
(5) A great part of the peritoneal epithelium.

General Considerations. In the history which has just been given of the development of the mesoblast, there are several points which appear to me to throw light upon the primitive origin of that layer. Before entering into these it is however necessary to institute a comparison between the history of the mesoblast in Elasmobranchs and in other Vertebrates, in order to distinguish as far as possible the primitive and the secondary characters present in the various groups.

Though the Mammals are to be looked on as the most differentiated group amongst the Vertebrates, yet in their embryonic history they retain many very primitive features, and, as has been recently shewn by Hensen[1], present numerous remarkable approximations to the Elasmobranchs. We find accordingly[2] that the primitive lateral plates of mesoblast undergo nearly the same changes in these two groups. In Mammals there is at first a continuous cavity extending through both the parietal and vertebral portions of each plate, and dividing the plates into a somatic and a splanchnic layer: this cavity is the primitive body-cavity. The vertebral portion of each plate with its contained cavity then becomes divided off from the parietal. The later development of these parts is not accurately known, but it seems that the outer portion of each vertebral plate, composed of two layers (somatic and splanchnic) enclosing between them a remnant of the primitive body-cavity, becomes separated off as a muscle-plate. The remainder forms a vertebral rudiment, &c. Thus the extension of the body-cavity into the vertebral portion of the mesoblast, and the constriction of the vertebral portion of the cavity from the remainder, are as distinctive features of Mammals as they are of the Elasmobranchs.

In Birds[3] the horizontal splitting of the mesoblast into somatic and splanchnic layers appears, as in Mammals, to extend at first to the summit of the protovertebræ, but these bodies become so early separated from the parietal plates that this fact has usually been overlooked or denied; but even on the second day of incubation the outer layer of the protovertebræ is continuous with the somatic layer of the lateral plates, and the inner layer and kernel of the protovertebræ with the splanchnic layer of the lateral plates[4]. After the isolation

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[1] *Zeitschrift f. Anat. Entwicklungsgeschichte*, Vol. I.

[2] Hensen *loc. cit.*

[3] For the history of protovertebræ and muscle-plates in Birds, vide *Elements of Embryology*, Foster and Balfour. The statement there made that the horizontal splitting of the mesoblast does not extend to the summit of the vertebral plate, must however be regarded as doubtful.

[4] Vide *Elements of Embryology*, p. 56.

of the protovertebræ the primitive position of the split which separated their somatic and splanchnic layers becomes obscured, but when on the third day the muscle-plates are formed they are found to be *constituted of two layers, an inner and an outer, which enclose between them a central cavity.* This remarkable fact, which has not received much attention, though noticeable in most figures, receives a simple explanation as a surviving rudiment on Darwinian principles. The central cavity of the muscle-plate is, in fact, a remnant of vertebral extension of the body-cavity, and is the same cavity as that found in the muscle-plates of Elasmobranchs. The two layers of the muscle-plate also correspond with the two layers present in Elasmobranchs, the one belonging to the somatic, the other to the splanchnic layer of mesoblast. The remainder of the protovertebræ internal to the muscle-plates is very large in Birds, and is the equivalent of that portion of the protovertebræ which in Elasmobranchs is split off to form the vertebral bodies[1] (Pl. x. fig. 6, 7, 8, *Vr*). Thus, though the history of the development of the mesoblast is not precisely the same for Birds as for Elasmobranchs, yet the differences between the two groups are of such a character as to prove in a striking manner that the Avian development is a derivation from a more primary form, like that of the Elasmobranchs.

According to the statements of Bambeke and Götte, the Amphibians present rather remarkable peculiarities in the development of their muscular system. Each side-plate of mesoblast is divided into a somatic and a splanchnic layer, continuous throughout the vertebral and parietal portions of the plate. The vertebral portions (protovertebræ) of the plates soon become separated from the parietal, and form an independent mass of cells constituted of two layers, which were originally continuous with the somatic and splanchnic layers of the parietal plates. The outer or somatic layer of the

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[1] Dr Götte, *Entwicklungsgeschichte der Unke*, p. 534, gives a different account of the development of the protovertebræ from that in the text. He states that the muscle-plates do not give rise to the main dorso-lateral muscles, but only to some superficial ventral muscles, while the dorso-lateral muscles are according to him formed from part of the kernel of the protovertebræ internal to the muscle-plates. The account given in the text is the result of my own investigations, and accords precisely with the recent statements of Professor Kölliker, *Entwicklungsgeschichte*, 1876.

vertebral plates is formed of a single row of cells, but the inner or splanchnic layer is made up of a central kernel of cells and an inner single layer. This central kernel is the first portion of the vertebral body to undergo any change, and it becomes converted into the main dorso-lateral muscles of the body, which apparently correspond with the muscles derived from the whole muscle-plate of the Elasmobranchs. From the inner layer of the splanchnic division there are next formed the main internal ventral muscles, rectus abdominis, &c., as well as the chief connective-tissue elements of the parts surrounding the spinal cord. The outer layer of the vertebral plates forms the dermis and sub-cutaneous connective tissue, as well as some of the superficial muscles of the trunk and the muscles of the limbs.

Dr Götte appears to think that the vertebral plates in Amphibians present a perfectly normal development very similar to that of other Vertebrates. The divergences between Amphibians and other Vertebrates appear, however, to myself, to be very great, and although the very careful account given by Dr Götte is probably to be relied on, yet some further explanation than he has offered of the development of these parts amongst the Amphibians would seem to be required.

A primary stage in which the two layers of the vertebral plates are continuous with the somatic and splanchnic layers of a body-wall is equally characteristic of Amphibians, Elasmobranchs and Mammals. In the subsequent development, however, a great difference between the types becomes apparent, for whereas in Elasmobranchs both layers of the vertebral plates combine to form the muscle-plates, out of which the great dorso-lateral muscles are formed, in Amphibians what appear to be the equivalent muscles are derived from a few of the cells (the kernel) of the inner layer of the vertebral plates only. The cells which form the lateral muscles in Amphibians might be thought to correspond in position with the cells which become, in Elasmobranchs, converted into the special early formed band of muscles (*m. p'.*), rather than, as their development seems to indicate, with the whole Elasmobranch muscle-plates[1].

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[1] The type of development of the muscle-plates of Amphibians would become identical with that of Elasmobranchs if their first-formed mass of muscle cor-

Osseous Fishes are stated to agree with Amphibians in the development of their protovertebræ and muscular system[1], but further observations on this point are required.

Though the development of the general muscular system and muscle-plates does not, according to existing statements, take place on quite the same type throughout the Vertebrate sub-kingdom, yet the comparison which has been instituted between Elasmobranchs and other Vertebrates appears to prove that there are one or two common features in their development, which may be regarded as primitive, and as having been inherited from the ancestors of Vertebrates. These features are (1) The extension of the body-cavity into the vertebral plates, and subsequent enclosure of this cavity between the two layers of the muscle-plates; (2) The primitive division of the vertebral plate into a somatic and a splanchnic layer, and the formation of a large part of the voluntary muscular system out of the splanchnic layer.

The ultimate derivation of the mesoblast forms one of the numerous burning questions of modern embryology, and there are advocates to be found for almost every one of the possible views the question admits of.

All who accept the doctrine of descent are agreed that primitively only two embryonic layers were present — the epiblast and the hypoblast—and that the mesoblast subsequently appeared as a distinct layer, after a certain complexity of organization had been attained.

The general agreement stops, however, at this point, and the greatest divergence of opinion exists with reference to all further questions which bear on the development of the mesoblast. There appear to be four possibilities as to the origin of this layer.

It may be derived:

(1) entirely from the epiblast,

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responded with the early-formed muscles of Elasmobranchs, and the remaining cells of both layers of the protovertebræ became in the course of development converted into muscle-cells indistinguishable from those formed at first. Is it possible that, owing to the distinctness of the first-formed mass of muscle, Dr Götte can have overlooked the fact that its subsequent growth is carried on at the expense of the adjacent cells of the somatic layer?

[1] Ehrlich, Ueber den peripher. Theil d. Urwirbel. *Archiv f. Mic. Anat.* Vol. XI.

(2) partly from the epiblast, and partly from the hypoblast,
(3) entirely from the hypoblast,
(4) or may have no fixed origin.

The fourth of these possibilities may for the present be dismissed, since it can be only maintained should it turn out that all the other views are erroneous. The first possibility is supported by the case of the Cœlenterata, and we might almost say by that of this group only[1].

Amongst the Cœlenterata the mesoblast, when present, is unquestionably a derivative of the epiblast, and when, as is frequently the case, a distinct mesoblast is not present, the muscle-cells form a specialized part of the epidermic cells.

The condition of the mesoblast in these lowly organized animals is exactly what might *à priori* have been anticipated, but the absence throughout the group of a true body-cavity, or specially developed muscular system of the alimentary tract, prevents the possibility of generalizing for other groups, from the condition of the mesoblast in this one.

In those animals in which a body-cavity and muscular alimentary tract are present, it would certainly appear reasonable to expect the mesoblast to be derived from both the primitive layers: the voluntary muscular system from epiblast, and the splanchnic system from the hypoblast. This view has been taken and strongly advocated by so distinguished. an embryologist as Professor Haeckel, and it must be admitted, that on *à priori* grounds there is much to recommend it; there are, however, so far as I am aware of, comparatively few observed facts in its favour.

Professor Haeckel's own objective arguments in support of his view are as follows:

(1) From the fact that some investigators derive the meso-

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[1] The most important other instances in addition to that of the Cœlenterata which can be adduced in favour of the epiblastic origin of the mesoblast are the Bird and Mammal, in which according to the recent observations of Hensen for the Mammal, and Kölliker for the Mammal and Bird, the mesoblast is split off from the epiblast. If the views I have elsewhere put forward about the meaning of the primitive groove be accepted, the derivation of the mesoblast from the epiblast in these instances would be apparent rather than real, and have no deep morphological significance for the present question.

Other instances may be brought forward from various groups, but none of these are sufficiently well confirmed to be of any value in the determination of the present question.

blast with absolute confidence from the hypoblast, while others do so with equal confidence from the epiblast, he concludes that it is really derived from both these layers.

(2) A second argument is founded on the supposed derivation of the mesoblast in Amphioxus from both epiblast and hypoblast. Kowalevsky's account (on which apparently Prof. Haeckel's[1] statements are based) appears to me, however, too vague, and his observations too imperfect, for much confidence to be placed in his statements on this head. It does not indeed appear to me that the formation of the layers in Amphioxus, till better known, can be used as an argument for any special view about this question.

(3) Professor Haeckel's own observations on the development of Osseous fish form a third argument in support of his views. These observations do not, however, accord with those of the majority of investigators, and not having been made by means of sections, require further confirmation before they can be definitely accepted.

(4) A fourth argument rests on the fact that the various embryonic layers fuse together to form the primitive streak or axis-cord in higher vertebrates. This he thinks proves that the mesoblast is derived from both the primitive layers. The primitive streak has, however, according to my views, quite another significance to that attributed to it by Professor Haeckel[2]; but in any case Professor Kölliker's researches, and on this point my own observations accord with his, appear to me to prove that the fusion which there takes place is only capable of being used as an argument in favour of an epiblastic origin of the mesoblast, and not of its derivation from both epiblast and hypoblast.

The objective arguments in favour of Professor Haeckel's views are not very conclusive, and he himself does not deny that the mesoblast as a rule apparently arises as a single and undivided mass from one of the two primary layers, and only subsequently becomes split into somatic and splanchnic strata. This original fusion and subsequent splitting of the mesoblast

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[1] Vide *Anthropogenie*, p. 197.

[2] Vide Self, Development of Elasmobranch Fishes, *Journal of Anat. and Phys.* Vol. x. note on p. 682, and also Review of Professor Kölliker's Entwicklungsgeschichte des Menschen u. d. höheren Thiere, *Journal of Anat. and Phys.* Vol. x.

is explained by him as a secondary condition, a possibility which cannot by any means be thrown on one side. It seems therefore worth while examining how far the history of the somatic and splanchnic layers of the mesoblast in Elasmobranchs and other Vertebrates accords with the supposition that they were primitively split off from the epiblast and the hypoblast respectively.

It is well to consider first of all what parts of the mesoblast of the body might be expected to be derived from the somatic and splanchnic layers on this view of their origin[1].

From the somatic layer of the mesoblast there would no doubt be formed the whole of the voluntary muscular system of the body, the dermis, the subcutaneous connective tissue, and the connective tissue between the muscles. It is probable also, though this point is less certain, that the skeleton would be derived from the somatic layer. From the splanchnic layer would be formed the connective tissue and muscular layers of the alimentary tract, and possibly also the vascular system.

Turning to the actual development of these parts, the discrepancy between theory and fact becomes very remarkable. From the somatic layer of the mesoblast, part of the voluntary muscular system and the dermis is no doubt derived, but the splanchnic layer supplies the material, not only for the muscular wall of the digestive canal and the vascular system, but also for the whole of the axial skeleton *and a great part of the voluntary muscular system of the body, including the first-formed muscles.* Though remarkable, it is nevertheless not inconceivable, that the skeleton might be derived from the splanchnic mesoblast, but it is very difficult to understand how there could be formed from it a part of the voluntary muscular system of the body indistinguishably fused with part of the muscular system derived from the somatopleure.

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[1] Professor Haeckel speaks of the splitting of the mesoblast in Vertebrates into a somatic and splanchnic layer as a secondary process (*Gastrula u. Eifurchung d. Thiere*), but does not make it clear whether he regards this secondary splitting as taking place along the old lines. It appears to me to be fairly certain that even if the original unsplit condition of the mesoblast is to be regarded as a secondary condition, yet that the splitting of this must take place along the old lines, otherwise a change in the position of the body-cavity in the adult would have to be supposed—an unlikely change producing unnecessary complication. The succeeding argument is based on the assumption that the unsplit condition is a secondary condition, but that the split which eventually appears in this occurs along the old lines, separating the primitive splanchnopleure from the primitive somatopleure.

No fact in my investigations comes out more clearly than that a great part of the voluntary muscular system is formed from the splanchnic layer of the mesoblast, yet this fact presents a most serious difficulty to the view that the somatic and splanchnic layers of the mesoblast in Vertebrates are respectively derived from the epiblast and hypoblast.

In spite, therefore, of general *à priori* considerations of a very convincing kind which tell in favour of the double origin of the mesoblast, this view is supported by so few objective facts, and there exists so powerful an array of facts against it, that at present, at least, it seems impossible to maintain it. The full strength of the facts against it will appear more fully in a review of the present state of our knowledge as to the development of the mesoblast in the different groups.

To this I now pass.

In a paper on the "Early stages of development in Vertebrates[1]" a short resumé was given of the development of the mesoblast throughout the animal kingdom, which it may be worth while repeating here with a few additions. So far as we know at present, the mesoblast is derived from the hypoblast in the following groups:

Echinoderms (Hensen, Agassiz, Metschnikoff, Selenka, Götte), Nematodes (Butschli), Sagitta (Kowalevsky, Butschli), Lumbricus and probably other Annelids (Kowalevsky), Brachiopoda (Kowalevsky), Crustaceans (Bobretzky), Insects (Kowalevsky, Ulianin, Dohrn), Myriapods (Metschnikoff), Tunicates (Kowalevsky, Kuppfer), Petromyzon (Owsjanikoff), Osseous fishes (Oellacher, Götte, Kowalevsky), Elasmobranchs (Self), Amphibians (Remak, Stricker, Götte).

The list includes members from the greater number of the groups of the animal kingdom; the most striking omissions being the Cœlenterates, Mollusks, and the Amniotic Vertebrates. The absence of the Cœlenterates has been already explained, and my grounds for regarding the Amniotic Vertebrates as apparent rather than real exceptions have also been pointed out. The Mollusks, however, remain as a large group, in which we as yet know very little as to the formation of the mesoblast.

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[1] *Quart. Jl. of Micros. Science*, July, 1875.

Dr Rabl[1], who seems recently to have studied the development of Lymnæus by means of sections, gives some figures shewing the origin of the mesoblast; they are, however, too diagrammatic to be of much service in settling the present question, and the memoirs of Professor Lankester[2] and Dr Fol[3] are equally inconclusive for this purpose, for, though they contain figures of elongated and branched mesoblast cells passing from the epiblast to the hypoblast, no satisfactory representations are given of the origin of these cells. I have myself observed in embryos of Turbo or Trochus similar elongated cells to those figured by Lankester and Fol, but was unable clearly to determine whence they arose. The most accurate observations which we have on this question are those of Professor Bobretzky[4]. In Nassa he finds that the three embryonic layers are all established during segmentation. The outermost and smallest cells form the epiblast, somewhat larger cells adjoining these the mesoblast, and the large yolk-cells the hypoblast. These observations do not, however, demonstrate from which of the primary layers the mesoblast is derived.

The evidence at present existing is clearly in favour of the mesoblast being, in almost all groups of animals, developed from the hypoblast, but strong as this evidence is, it has not its full weight unless the actual manner in which the mesoblast is in many groups derived from the hypoblast, is taken into consideration. The most important of these are the Echinoderms, Brachiopods and Sagitta.

In the Echinoderms the mesoblast is in part formed by cells budded off from the hypoblast, *the remainder, however, arises as one or more diverticula of the alimentary tract.* From the separate cells first budded off there are formed the cutis, part of the connective tissue and the calcareous skeleton[5]. The diverticula from the alimentary cavity form the water-vascular system and the somatic and splanchnic layers of mesoblast. *The cavity of*

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[1] *Jenaische Zeitschrift*, Vol. IX.

[2] *Quart. Jl. of Micros. Science*, Vol. XXV. 1874, and *Phil. Trans.* 1875.

[3] *Archives de Zoologie*, Vol. IV.

[4] *Archiv f. Micr. Anat.* Vol. XIII.

[5] The recent researches of Selenka, *Zeitschrift f. Wiss. Zoologie*, Vol. XXVII. 1876, demonstrate that in Echinoderms the muscles are derived from the cells first split off from the hypoblast, and that the diverticula only form the water-vascular system and the epithelial lining of the body-cavity.

the diverticula after the separation of the water-vascular system, forms the body-cavity. The outer lining layer of the cavity forms the somatic layer of mesoblast and the voluntary muscles; the inner lining layer the splanchnic mesoblast which unites with the epithelium of the alimentary tract. Though this fundamental arrangement would seem to be universal amongst Echinoderms, considerable variations of it are exhibited in different groups.

There is *one* outgrowth from the alimentary tract in Synapta; *two* in Echinoids, Asteroids and Ophiura; *three* in Comatula, and four (?) in Amphiura. The cavity of the outgrowth usually forms the body-cavity, but sometimes in Ophiura and Amphiura (Metschnikoff) the outgrowths are from the first or soon become solid, and only secondarily acquire a cavity, which is however homologous with the body-cavity of the other groups.

In Sagitta[1] the formation of the mesoblast and the alimentary tract takes place in nearly the same fashion as in the Echinoderms. The simple invaginate alimentary cavity becomes divided into three lobes, a central and two lateral. The two lateral lobes are gradually more and more constricted off from the central one, and become eventually quite separated from it; their cavities remain independent, *and form in the adult the body-cavity*, divided by a mesentery into two distinct lateral sections. *The inner layer of each of the two lateral lobes forms the mesoblast of the splanchnopleure, the outer layer the mesoblast of the somatopleure.* The central division of the primitive gastræa cavity remains as the alimentary tract of the adult.

The remarkable observations of Kowalevsky[2] on the development of the Brachiopoda have brought to light the unexpected fact that in two genera at least (Argiope and Terebratula) the mesoblast and body-cavity develope as paired constrictions from the alimentary tract in a manner almost identically the same as in Sagitta.

It thus appears that, so far as can be determined from the facts at our disposal, the mesoblast in almost all cases is derived

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[1] Kowalevsky, Würmer u. Arthropoden, *Mém. Acad. Pétersbourg*, 1871.

[2] Zur Entwicklungsgeschichte d. Brachiopoden Protokoll d. Ersten Session der Versammlung Russischer Naturforscher i. Kasan, 1873. Published in *Kaiserliche Gesellschaft Moskau*, 1874 (Russian). Abstracted in Hoffmann and Schwalbe, *Jahresbericht f.* 1873.

from the hypoblast, and in three widely separated groups it arises as a pair of diverticula from the alimentary tract, each diverticulum containing a cavity which eventually becomes the body-cavity. I have elsewhere suggested[1] that the origin of the mesoblast from alimentary diverticula is to be regarded as primitive for all higher animals, and that the more general cases in which the mesoblast becomes split off, as an undivided layer, from the hypoblast, are in reality derivates from this. The chief obstacle in the way of this view arises from the difficulty of understanding how the whole voluntary muscular system can have been derived at first from the alimentary tract. That part of a voluntary system of muscles might be derived from the contractile diverticula of the alimentary canal attached to the body-wall is not difficult to understand, but it is not easy to believe that the secondary system so formed could completely replace the primitive muscular system, derived, as it must have been, from the epiblast. In my paper above quoted will be found various speculative suggestions for removing this difficulty, which I do not repeat here. If it be granted, however, that in Sagitta, Brachiopods, and Echinoderms we have genuine examples of the formation of the whole mesoblast from alimentary diverticula, it is easy to see how the formation of the mesoblast in Vertebrates may be a second derivate from an origin of this nature.

An attempt has been already made to shew that the mesoblast in Elasmobranchs is formed in a very primitive fashion, and for this reason the Elasmobranchs appear to be especially adapted for determining whether any signs are exhibited of a derivation of the mesoblast as paired diverticula of the alimentary tract. There are, it appears to me, several such features. In the first place, the mesoblast is split off from the hypoblast not as a single mass but as a pair of distinct masses, comparable with the paired diverticula already alluded to. Secondly, the body-cavity when it appears in the mesoblast plates, *does not arise as a single cavity, but as a pair of cavities, one for each plate of mesoblast,* and these cavities remain permanently distinct in some parts of the body, and nowhere unite till a comparatively late period. Thirdly, the primitive

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[1] Comparison of Early Stages, *Quart. Jl. Micros. Science*, July, 1875.

body-cavity of the embryo is not confined to the region in which a body-cavity exists in the adult, *but extends to the summit of the muscle-plates,* at first separating parts which become completely fused in the adult to form the great lateral muscles of the body. It is difficult to understand how the body-cavity could have such an extension as this, on the supposition that it represents a primitive split in the mesoblast between the wall of the gut and the body-wall; but its extension to this part is quite intelligible, on the supposition that it represents the cavities of two diverticula of the alimentary tract, from whose muscular walls the voluntary muscular system has been derived. Lastly, I would point out that the derivation of part of the muscular system from what appears as the splanchnopleure is quite intelligible on the assumed hypothesis, but, as far as I see, on no other.

Such are the main features presented by the mesoblast in Elasmobranchs, which favour the view of its having originally formed the walls of the alimentary diverticula. Against this view of its nature are the facts (1) of the mesoblast plates being at first solid, and (2), as a consequence of this, of the body-cavity never communicating with the alimentary canal. These points, in view of our knowledge of embryological modifications, cannot be regarded as great difficulties to my view. We have many examples of organs, which, though in most cases arising as involutions, yet appear in other cases as solid ingrowths. Such examples are afforded by the optic vesicle, auditory vesicle, and probably also by the central nervous system, of Osseous Fish. In most Vertebrates these organs are formed as hollow involutions from the exterior; in Osseous Fish, however, as solid involutions, in which a cavity secondarily appears.

The segmental duct of Elasmobranchs or the Wolffian duct (segmental duct) of Birds are cases of a similar kind, being organs which must originally have been formed as hollow involutions, but which now arise as solid bodies.

Only one more instance of this kind need be cited, taken from the Echinoderms.

The body-cavity and the mesoblast investing it arise in the case of most Echinoderms as hollow involutions of the alimentary tract, but in some exceptional groups, Ophiura and Amphiura, are stated to be solid at first and only subsequently to become hollow. Should the accuracy of Metschnikoff's account of this point be confirmed, an almost exact parallel to what has been supposed by me to have occurred with the mesoblast in Elasmobranchs, and other groups, will be supplied.

The tendency of our present knowledge appears to be in favour of regarding the body-cavity in Vertebrates as having been primitively the cavity of alimentary diverticula, and the mesoblast as having formed the walls of the diverticula.

This view, to say the least of it, suits the facts which we know far better than any other theory which has been proposed, and though no doubt the *à priori* difficulties in its way are very great, yet it appears to me to be sufficiently strongly supported to deserve the attention of investigators. In the meantime, however, our knowledge of invertebrate embryology is so new and imperfect that no certainty on a question like that which has just been discussed can be obtained; and any generalizations made at present are not unlikely to be upset by the discovery of fresh facts.

The only other point in connection with the mesoblast which I would call attention to is the formation of the vertebral bodies.

My observations confirm those of Remak and Gegenbaur, shewing that there is a primary segmentation of the vertebral bodies corresponding to that of the muscle-plates, followed by a secondary segmentation in which the central lines of vertebral bodies are opposite the partitions between the muscle-plates.

The explanation of these changes is not difficult to find. The primary segmentation of the body is that of the muscle-plates, which must have been present at a time when the vertebral bodies had no existence. As soon however as the notochordal sheath was required to be strong as well as flexible, it necessarily became divided into a series of segments.

The conditions under which the lateral muscles can cause the flexure of the vertebral column are clearly that each muscle-segment shall be capable of acting on two vertebræ; and this condition can only be fulfilled when the muscle-segments are opposite the intervals between the vertebræ. Owing to this necessity, when the vertebral segments became formed, their centres corresponded, not with the centres of the muscle-plates, but with the inter-muscular septa.

These considerations fully explain the secondary segmentation of the vertebræ by which they become opposite the inter-muscular septa. On the other hand, the primary segmentation is clearly a remnant of the time when no vertebral bodies were present, and has no greater morphological significance than the fact that the cells to form the unsegmented investment of the notochord were derived from the segmented muscle-plates, and only secondarily became fused into a continuous tube.

The Urino-genital System.

The first traces of the urinary system become visible at about the time of the appearance of the third visceral cleft. At about this period the somatopleure and splanchnopleure become more or less fused together at the level of the dorsal aorta, and thus, as has been already mentioned, each of the original plates of mesoblast becomes divided into a vertebral plate and lateral plate (Pl. x. fig. 6). The mass of cells resulting from this fusion corresponds with Waldeyer's intermediate cell-mass in the Fowl.

At about the level of fifth protovertebra the first trace of the urinary system appears.

From the intermediate cell-mass a solid knob grows outwards towards the epiblast (woodcut, fig. 4, *pd*). This knob consists at first of 20—30 cells, which agree in character with the neighbouring cells of the intermediate cell-mass, and are at this period rounded. It is mainly, if not entirely, derived from the somatic layer of the mesoblast.

From this knob there grows backwards a solid rod of cells which keeps in very close contact with the epiblast, and rapidly diminishes in size towards its posterior extremity. Its hindermost part consists in section of at most one or two cells. It keeps so close to the epiblast that it might be supposed to be derived from that layer were it not for the sections shewing its origin from the knob above mentioned. We have in this rod the commencement of what I have elsewhere[1] called the segmental duct.

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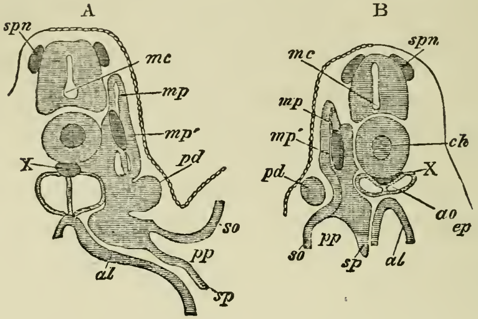
[1] Urinogenital Organs of Vertebrates, *Journ. of Anat. and Phys.* Vol. x.

Fig. 4.—Two sections of a Pristiurus Embryo with three visceral clefts.



The sections are to shew the development of the segmental duct ((*pd*) or primitive duct of the kidneys. In *A* (the anterior of the two sections) this appears as as a solid knob projecting towards the epiblast. In *B* is seen a section of the column which has grown backwards from the knob in *A*. *spn.* rudiment of a spinal nerve; *mc.* medullary canal; *ch.* notochord; *X.* string of cells below the notochord; *mp.* muscle-plate; *mp'.* specially developed portion of muscle-plate; *ao.* dorsal aorta; *pd.* segmental duct. *so.* somatopleura; *sp.* splanchnopleura; *pp.* pleuroperitoneal or body-cavity; *ep.* epiblast; *al.* alimentary canal.

My observations shew that the segmental duct is developed in the way just described in both Pristiurus and Torpedo. Its origin in Pristiurus is shewn in the adjoining woodcut, and in Torpedo in Plate X. fig. 7*sd*.

At a stage somewhat older than I, the condition of the segmental duct has not very materially altered. It has increased considerably in length, and the knob at its front end is both absolutely smaller, and also consists of fewer cells than before (Pl. X. fig. 7 *sd*). These cells have become more columnar, and have begun to arrange themselves radially; thus indicating the early appearance of the lumen of the duct. The cells forming the front part of the rod, as well as those of the knob, commence to exhibit a columnar character, but in the hinder part of the rod the cells are still rounded. In no part of it has a lumen appeared.

At this period also the knob, partly owing to the commencing separation of the muscle-plate from the remainder of the mesoblast, begins to pass inwards and approach the pleuroperitoneal cavity.

At the same stage the first not very distinct traces of the remainder of the urinary system become developed. These appear in the form of solid outgrowths from the intermediate cell-mass just at the most dorsal part of the body-cavity.

The outgrowths correspond in numbers with the vertebral segments, and are at first quite disconnected with the segmental duct. At this stage they are only distinctly visible in the first few segments behind the front end of the segmental duct. A full description of them will come more conveniently in the next stage.

By a stage somewhat earlier than K important changes have taken place in the urinary system.

The segmental duct has acquired a lumen in its anterior portion, which opens at its front end into the body-cavity. (Pl. XI. fig. 9 *sd*). The lumen is formed by the columnar cells spoken of in the last stage, acquiring a radiating arrangement round a central point, at which a small hole appears. After the lumen has once become formed, it rapidly increases in size.

The duct has also grown considerably in length, but its hind extremity is still as thin, and lies as close to the epiblast, as at first. The segmental involutions which commenced to be formed in the last stage, have now appeared for every vertebral segment along the whole length of the segmental duct, and even for two or three segments behind this.

They are simple independent outgrowths arising from the outer and uppermost angle of the body-cavity, and are at first almost without a trace of a lumen, though their cells are arranged as two layers. They grow in such a way as to encircle the oviduct on its inner and upper side (Pl. X. fig. 8 and Pl. XI. fig. 14 *b. st*). When the hindermost ones are formed, a slight trace of a lumen is perhaps visible in the front ones. At a stage slightly subsequent to this, in Scyllium Canicula, I noticed 29 of them; the first of them arising in the segment immediately behind the front end of the oviduct (Pl. XI. fig. 17 *st*), and two of them being formed in segments just posterior to the hinder extremity of the oviduct.

Pl. XI. fig. 16 and 18 represent two longitudinal sections shewing the segmental nature of the involutions and their relation to the segmental duct.

Many of the points which have been mentioned can be seen by referring to Pl. X. and XI. Anteriorly the segmental duct opens into the pleuro-peritoneal cavity. In the sections behind this there may be seen the segmental duct with a distinct lumen, and also a pair of segmental involutions (Pl. XI. fig. 14 *a*). In the still posterior sections the segmental duct would be quite without a lumen, and would closely adjoin the epiblast.

It seems not out of place to point out that the modes of the development of the segmental duct and of the segmental involutions are strikingly similar. Both arise as solid involutions, from homologous parts of the mesoblast. The segmental duct arises in the vertebral segment immediately in front of that in which the first segmental involution appears; *so that the segmental duct appears to be equivalent to a single segmental involution.*

The next stage corresponds with the first appearance of the external gills. The segmental duct now communicates by a wide opening with the body-cavity (Pl. XI. fig. 9 *sd*). It possesses a lumen along its whole length up to the extreme hind end (Pl. XI. fig. 9*a*). It is, however, at this hinder extremity that the most important change has taken place. This end has grown downwards towards that part of the alimentary canal which still lies behind the anus. This downgrowth is beginning to shew distinct traces of a lumen, and will appear in the next stage as one of the horns by which the segmental ducts communicate with the cloaca (Pl. XI. fig. 9 *b*). All the anterior segmental involutions have now acquired a lumen. But this is still absent in the posterior ones (Pl. XI. fig. 9 *a*).

Owing to the disappearance of the body-cavity in the region behind the anus, the primitive involutions there remain as simple masses of cells still disconnected with the segmental duct (Pl. XI. fig. 9 *b*, 9 *c* and 9 *d*).

Primitive Ova. The true generative products make their first appearance as the *primitive ova* between stages I and K.

In the sections of one of my embryos of this stage they are especially well shewn, and the following description is taken from those displayed in that embryo.

They are confined to the region which extends posteriorly nearly to the end of the small intestine and anteriorly to the abdominal opening of the segmental duct.

Their situation in this region is peculiar. There is no trace of a distinct genital ridge, but the ova mainly lie in the dorsal portion of the mesentery, and therefore in a part of the mesoblast which distinctly belongs to the splanchnopleure (Pl. XI. fig. 14*a*). Some are situated external to the segmental involutions; and others again, though this is not common, in a part of the mesoblast which distinctly belongs to the body-wall (Pl. XI. fig. 14 *b*).

The portion of mesentery in which the primitive ova are most densely aggregated, corresponds to the future position of the genital ridge, but the other positions occupied by ova are quite outside this. Some ova are in fact situated on the outside of the segmental duct and segmented tubes, and must therefore effect a considerable migration before reaching their final positions in the genital ridge on the inner side of the segmental duct (Pl. XI. fig. 14 *b*).

The condition of the tissue in which the ova appear may at once be gathered from an examination of the figures given. It consists of an irregular epithelium of cells partly belonging to the somatopleure and partly to the splanchnopleure, but passing uninterruptedly from one layer to the other. The cells which compose it are irregular in shape, but frequently columnar (Pl. XI. fig. 14 *a* and 14 *b*).

They are formed of a nucleus which stains deeply, invested by a *very delicate* layer of protoplasm. At the junction of somatopleure and splanchnopleure they are more rounded than elsewhere. Very few loose connective-tissue cells are present. The cells just described vary from ·008 Mm. to ·01 Mm. in diameter.

The primitive ova are situated amongst them and stand out with extraordinary clearness, to which justice is hardly done in my figures.

The normal full-sized ova exhibit the following structure. They consist of a mass of somewhat granular protoplasm of irregular, but more or less rounded, form. Their size varies from ·016—·036 Mm. In their interior a nucleus is present, which varies from ·012—·016 Mm., but its size as a rule bears *no* relation to the size of the containing cell.

This is illustrated by the subjoined list of measurements.

The numbers given refer to degrees on my micrometer scale.

Since it is the ratio alone which it is necessary to call attention to, the numbers are not reduced to decimals of a millimeter. Each degree of my scale is equal, however, with the object glass employed, to ·002 Mm.

Size of Primitive ova in degrees of micrometer scale with F. ocul 2.	Size of nucleus of Primitive ova in degrees of micrometer scale with F. ocul 2.
10	8
13	8
13	8
14	7
15	7
13	7½
11	8
16	5½
12	7
10	7
15	6
13	6
12	7

This series brings out the result I have just mentioned with great clearness.

In one case we find a cell has three times the diameter of the nucleus 16 : 5½; in another case 10 : 8, the nucleus has only a slightly smaller diameter than the cell. The irrationality of the ratio is fairly shewn in some of my figures, though none of the largest cells with very small nuclei have been represented.

The nuclei are granular, and stain fairly well with hæmatoxylin. They usually contain a single deeply stained nucleolus, but in many cases, especially where large (and this independently of the size of the cell), they contain two nucleoli (Pl. XI. fig. 14 *c* and 14 *d*), and are at times so lobed as to give an apparent indication of commencing division.

A multi-nucleolar condition of the nuclei, like that figured by Götte[1], does not appear till near the close of embryonic life, and is then found equally in the large ova and in those not larger than the ova which exist at this early date.

As regards the relation of the primitive ova to each other and the neighbouring cells, there are a few points which deserve attention. In the first place, the ova are, as a rule, collected in masses at particular points, and not distributed uniformly (fig. 14 *a*.) The masses in some cases appear as if they had

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[1] *Entwicklungsgeschichte der Unke*, Pl. I. fig. 8.

resulted from the division of one primitive ovum, but can hardly be adduced as instances of a commencing coalescence; since if the ova thus aggregated were to coalesce, an ovum would be produced of a very much greater size than any which is found during the early stages. Though at this stage no indication is present of such a coalescence of cells to form ova as is believed to take place by Götte, still the origin of the primitive ova is not quite clear. One would naturally expect to find a great number of cells intermediate between primitive ova and ordinary columnar cells. Cells which may be intermediate are no doubt found, but not nearly so frequently as might have been anticipated. One or two cells are shewn in Pl. XI. fig. 14 *a*. *x*, which are perhaps of an intermediate character; but in most sections it is not possible to satisfy oneself that any such intermediate cells are present.

In one case what appeared to be an intermediate cell was measured, and presented a diameter of ·012 Mm. while its nucleus was ·008 Mm. Apart from certain features of the nucleus, which at this stage are hardly very marked, the easiest method of distinguishing a primitive ovum from an adjacent cell is the presence of a large quantity of protoplasm around the nucleus. The nucleus of one of the smallest primitive ova is not larger than the nucleus of an ordinary cell (being about ·008 Mm. in both). It is perhaps the similarity in the size of the nuclei which renders it difficult at first to distinguish developing primitive ova from ordinary cells. Except with the very thinnest sections a small extra quantity of protoplasm around a nucleus might easily escape detection, and the developing cell might only become visible when it had attained to the size of a small typical primitive ovum.

It deserves to be noticed that the nuclei even of some of the largest primitive ova scarcely exceed the surrounding nuclei in size. This appears to me to be an argument of some weight in shewing that the great size of primitive ova is not due to the fact of their having been formed by a coalescence of different cells (in which case the nucleus would have increased in the same proportion as the cell); but to an increase by a normal method of growth in the protoplasm around the nucleus.

It appears to me to be a point of great importance certainly to determine whether the primitive ova arise by a metamorphosis of adjoining cells, or may not be introduced from elsewhere. In some of the lower animals, *e. g.* Hydrozoa, there is no question that the ova are derived from the epiblast; we might therefore expect to find that they had the same origin in Vertebrates. Further than this, ova are frequently capable in a young state of executing amœboid movements, and accordingly of migrating from one layer to another. In the Elasmobranchs the primitive ova exhibit in a hardened state an irregular form which might appear to indicate that they possess a power of altering their shape, a view which is further supported by some of them being at the present stage situated in a position very different from that which they eventually occupy, and which they can only reach by migration. If it could be shewn that there were no intermediate stages between the primitive ova and the adjoining cells (their migratory powers being admitted) a strong presumption would be offered in favour of their having migrated from elsewhere to their present position. In view of this possibility I have made some special investigations, which have however led to no very satisfactory results. There are to be seen in the stages immediately preceding the present one, numerous cells in a corresponding position to that of the primitive ova, which might very well be intermediate between the primitive ova and ordinary cells, but which offer no sufficiently well marked features for a certain determination of their true nature.

In the particular embryo whose primitive ova have been described these bodies were more conspicuous than in the majority of cases, but at the same time they presented no special or peculiar characters.

In a somewhat older embryo of Scyllium the cells amongst which the primitive ova lay had become very distinctly differentiated as an epithelium (the germinal epithelium of Waldeyer) well separated by what might almost be called a basement membrane from the adjoining connective-tissue cells. Hardly any indication of a germinal ridge had appeared, but the ova were more definitely confined than in previous embryos to the restricted area which eventually forms this. The ova on the average were somewhat smaller than in the previous cases.

In several embryos intermediate in age between the embryo whose primitive ova were described at the commencement of this section and the embryo last described, the primitive ova presented some peculiarities, about the meaning of which I am not quite clear, but which may perhaps throw some light on the origin of these bodies.

Instead of the protoplasm around the nucleus being clear or slightly granular, as in the cases just described, it was filled in the most typical instances with numerous highly refracting bodies resembling yolk-spherules. In osmic acid specimens (Pl. XI. fig. 15) these stain very darkly, and it is then as a rule very difficult to see the nucleus; in specimens hardened in picric acid and stained with hæmatoxylin these bodies are stained of a deep purple colour, but the nucleus can in most cases be distinctly seen. In addition to the instances in which the protoplasm of the ova is quite filled with these bodies, there are others in which they only occupy a small area adjoining the nucleus (Pl. XI. fig. 15 *a*), and finally some in which only one or two of these bodies are present. The protoplasm of the primitive ova appears in fact to present a series of gradations between a state in which it is completely filled with highly refracting spherules and one in which these are completely absent.

This state of things naturally leads to the view that the primitive ova, when they are first formed, are filled with these spherules, which are probably yolk-spherules, but that they gradually lose them in the course of development. Against this interpretation is the fact that the primitive ova in the younger embryo first described are completely without these bodies; this embryo however unquestionably presented an abnormally early development of the ova; and I am satisfied that embryos present considerable variations in this respect.

If the primitive ova are in reality in the first instance filled with yolk-spherules, the question arises as to whether, considering that they are the only mesoblast cells filled at this period with yolk-spherules, we must not suppose that they have migrated from some peripheral part of the blastoderm into their present position. To this question I can give no satisfactory answer. Against a view which would regard the spherules in the protoplasm as bodies which appear subsequently to the first formation of the ova, is the fact that hitherto no instances in which these spherules were present have been met with in the late stages of development; and they seem therefore to be confined to the first stages.

Notochord.

The changes undergone by the notochord during this period present considerable differences according to the genus examined. One type of development is characteristic of Scyllium and Pristiurus; a second type, of Torpedo.

My observations being far more complete for Scyllium and Pristiurus than for Torpedo, it is to the two former genera only that the following account applies, unless the contrary is expressly stated. Only the development of the parts of the notochord in the trunk are here dealt with; the cephalic section of the notochord is treated of in a subsequent section.

During stage G the notochord is composed of flattened cells arranged vertically, rendering the histological characters of the notochord difficult to determine in transverse sections. In longitudinal sections, however, the form and arrangement of the cells can be recognised with great ease. At the beginning of stage G each cell is composed of a nucleus invested by granular protoplasm frequently vacuolated and containing in suspension numerous yolk-spherules. It is difficult to determine whether there is only one vacuole for each cell, or whether in some cases there may not be more than one.

Round the exterior of the notochord there is present a distinct though delicate cuticular sheath.

The vacuoles are at first small, but during stage G rapidly increase in size, while at the same time the yolk-spherules completely vanish from the notochord.

As a result of the rapid growth of the vacuoles, the nuclei, surrounded in each case by a small amount of protoplasm, become pushed to the centre of the notochord, the remainder of the protoplasm being carried to the edge. The notochord thus becomes composed during stages H and I (Pl. x. fig. 4—6) of a central area mainly formed of nuclei with a small quantity of protoplasm around them, and of a thin peripheral layer of protoplasm without nuclei, the widish space between the two being filled with clear fluid. The exterior of the cells is indurated, so that they may be said to be invested by a membrane[1]; the cells themselves have a flattened form, and each extends from the edge to the centre of the notochord, the long axis of each being rather greater than half the diameter of the cord.

The nuclei of the notochord are elliptical vesicles, consisting of a membrane filled with granular contents, amongst which is situated a distinct nucleolus. They stain deeply with hæmatoxylin. Their long diameter in Scyllium is about 0·02 Mm.

The diameter of the whole notochord in Pristiurus during stage I is about 0·1 Mm. in the region of the back, and about 0·08 Mm. near the posterior end of the body.

Owing to the form of its constituent cells, the notochord presents in transverse sections a dark central area surrounded by a lighter peripheral one, but its true structure cannot be unravelled without the assistance of longitudinal sections. In these (Pl. XI. fig. 10) the nuclei form an irregular double row in the centre of the cord. Their outlines are very clear, but those of the individual cells cannot for certain be made out. It is, however, easy to see that the cells have a flattened and wedge-shaped form, with the narrow ends overlapping and interlocking at the centre of the notochord.

By the close of stage I the cuticular sheath of the notochord has greatly increased in thickness.

During the period intermediate between stages I and K the notochord undergoes considerable transformations. Its cells cease to be flattened, and become irregularly polygonal, and appear but slightly more compressed in longitudinal sections than in transverse ones. The vacuolation of the cells proceeds rapidly, and there is left in each cell only a very thin layer of protoplasm around the nucleus. Each cell, as in the earlier stages, is bounded by a membrane-like wall.

Accompanying these general changes special alterations take place in the distribution of the nuclei and the protoplasm. The nuclei, accompanied by protoplasm, gradually leave the centre and migrate towards the periphery of the notochord. At the same time the protoplasm of the cells forms a special layer in contact with the investing sheath.

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[1] This membrane is better looked upon, as is done by Gegenbaur and Götte, as intercellular matter.

The changes by which this takes place can easily be followed in longitudinal sections. In Pl. XI. fig. 11 the migration of the nuclei has commenced. They are still, however, more or less aggregated at the centre, and very little protoplasm is present at the edges of the notochord. The cells, though more or less irregularly polygonal, are still somewhat flattened. In Pl. XI. fig. 12 the notochord has made a further progress. The nuclei now mainly lie at the side of the notochord, where they exist in a somewhat shrivelled state, though still invested by a layer of protoplasm.

A large portion of the protoplasm of the cord forms an almost continuous layer in close contact with the sheath, which is more distinctly visible in some cases than in others.

While the changes above described are taking place the notochord increases in size. At the age of fig. 11 it is in the anterior part of the body of Pristiurus about 0·11 Mm. At the age of fig. 12 it is in the same species 0·12 Mm., while in Scyllium Stellare it reaches about 0·17 Mm.

During stage K (Pl. X. fig. 8) the vacuolation of the cells of the notochord becomes even more complete than during the earlier stages, and in the central cells hardly any protoplasm is present, though a starved nucleus surrounded by a little protoplasm may be found in an occasional corner.

The whole notochord becomes very delicate, and can with great difficulty be conserved whole in transverse sections.

The layer of protoplasm which appeared during the last stage on the inner side of the cuticular membrane of the notochord becomes during the present stage a far thicker and more definite structure. It forms a continuous layer with irregular prominences on its inner surface; and contains numerous nuclei. The layer sometimes presents in transverse sections hardly any indication of a division into a number of separate cells, but in longitudinal sections this is generally very obvious. The cells are directed very obliquely forwards, and consist of an oblong nucleus invested by protoplasm. The layer formed by them is very delicate and very easily destroyed. In one example its thickness varied from ·004 to ·006 Mm., in another it reached ·012 Mm. The thickness of the cuticular membrane is about ·002 Mm. or rather less.

The diameter of a notochord in the anterior part of the body of a Pristiurus embryo of this stage is about 0·21 Mm. Round the exterior of the notochord the mesoblast cells are commencing to arrange themselves as a special sheath.

In Torpedo the notochord at first presents the same structure as in Pristiurus, *i. e.* it forms a cylindrical rod of flattened cells.

The vacuolation of these cells does not however commence till a relatively very much later period than in Pristiurus, and also presents a very different character (Pl. x. fig. 7).

The vacuoles are smaller, more numerous, and more rounded than in the other genera, and there can be no question that in many cases there is more than one vacuole in a cell. The most striking point in which the notochord of Torpedo differs from that of Pristiurus consists in the fact that in Torpedo there is never any aggregation of the nuclei at the centre of the cord, but the nuclei are always distributed uniformly through it. As the vacuolation proceeds the differences between Torpedo and the other genera become less and less marked. The vacuoles become angular in form, and the cells of the cord cease to be flattened, and become polygonal.

At my final stage for Torpedo (slightly younger than K) the only important feature distinguishing the notochord from that of Pristiurus, is the absence of any signs of nuclei or protoplasm passing to the periphery. Around the exterior of the cord there is early found in Torpedo a special investment of mesoblastic cells.

CHAPTER VII.

GENERAL DEVELOPMENT OF THE TRUNK FROM STAGE H TO THE CLOSE OF EMBRYONIC LIFE.

External Epiblast.

THE change already alluded to in the previous chapter (p. 99) by which the external epiblast or epidermis becomes divided into two layers, is completed before the close of stage L.

In the tail region at this stage three distinct strata may be recognized in the epidermis. (1) An outer stratum of flattened horny cells, which fuse together to form an almost continuous membrane. (2) A middle stratum of irregular partly rounded and partly flattened cells. (3) An internal stratum of columnar cells, bounded towards the mesoblast by a distinct basement membrane (Pl. XII. fig. 8), unquestionably pertaining to the epiblast. This layer is especially thickened in the terminal parts of the paired fins (Pl. XII. fig. 1). The two former of these strata together constitute the epidermic layer of the skin, and the latter the mucous layer.

In the anterior parts of the body during stage L the skin only presents two distinct strata, viz. an inner somewhat irregular layer of rounded cells, the mucous layer, and an outer layer of flattened cells (Pl. XII. fig. 8).

The remaining history of the external epiblast, consisting as it does of a record of the gradual increase in thickness of the epidermic strata, and a topographical description of its variations in structure and thickness in different parts, is of no special interest and need not detain us here.

In the late embryonic periods subsequent to stage Q the layers of the skin cease to be so distinct as at an earlier period, partly owing to the innermost layer becoming less columnar, and partly to the presence of a large number of mucous cells, which have by that stage made their appearance.

I have followed with some care the development of the placoid scales, but my observations so completely accord with those of Dr O. Hertwig[1], that it is not necessary to record them. The so-called enamel layer is a simple product of the thickening and calcification of the basement membrane, and since this membrane is derived from the mucous layer of epidermis, the enamel is clearly to be viewed as an epidermic product. There is no indication of a gradual conversion of the bases of the columnar cells forming the mucous layer of the epidermis into enamel prisms, as is frequently stated to occur in the formation of the enamel of the teeth in higher Vertebrates.

Lateral line.

The lateral line and the nervous structures appended to it have been recently studied from an embryological point of view by Götte[2] in Amphibians and by Semper[3] in Elasmobranchs.

The most important morphological result which these two distinguished investigators believe themselves to have arrived at is the direct derivation of the lateral nerve from the ectoderm. On this point there is a complete accord between them, and Semper especially explains that it is extremely easy to establish the fact.

As will appear from the sequel, I have not been so fortunate as Semper in elucidating the origin of the lateral nerve, and my observations bear an interpretation not in the least in accordance with the views of my predecessors, though not perhaps quite conclusive against them.

It must be premised that two distinct structures have to be dealt with, viz. the *lateral line* formed of modified epidermis, and the *lateral nerve* whose origin is in question.

The lateral line is the first of the two to make its appearance, at a stage slightly subsequent to K, in the form of a linear thickening of the inner row of cells of the external epiblast, on each side, at the level of the notochord.

This thickening, in my youngest embryo in which it is found, has but a very small longitudinal extension, being

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[1] *Jenaische Zeitschrift*, Vol. VIII.

[2] *Entwicklungsgeschichte d. Unke.*

[3] *Urogenital-system d. Selachier.* Semper's *Arbeiten*, Bd. II.

present through about 10 thin sections in the last part of the head and first part of the trunk. The thickening, though short, is very broad, measuring about 0·28 Mm. in transverse section, and presents no signs of a commencing differentiation of nervous structures. The large intestinal branch of the vagus can be seen in all the anterior sections in close proximity to this line, and appears to me to give off to it posteriorly a small special branch which can be traced through a few sections, vide Pl. XII. fig. 2 *n.l.* But this branch is not sufficiently well marked to enable me to be certain of its real character. In any case the posterior part of the lateral line *is absolutely without any adjoining nervous structures or traces of such.*

The rudiment of the epidermic part of the lateral line is formed of specially elongated cells of the mucous layer of the epiblast, but around the bases of these certain rounder cells of a somewhat curious appearance are intercalated.

There is between this and my next youngest embryo an unfortunately large gap with reference to the lateral line, although in almost every other respect the two embryos might be regarded as belonging to the same stage. The lateral line in the older embryo extends from the hind part of the head to a point well behind the anus, and is accompanied by a nerve for at least two-thirds of its length.

In the foremost section in which it appears the intestinal branch of the vagus is situated not far from it, *and may be seen at intervals giving off branches to it.* There is no sign that these are otherwise than perfectly normal branches of the vagus. Near the level of the last visceral cleft the intestinal branch of the vagus gives off a fair-sized branch, which from the first occupies a position close to the lateral line though well within the mesoblast (Pl. XII. fig. 3*a*, *n.l*). This branch is the lateral nerve, and though somewhat larger, is otherwise much like the nerve I fancied I could see originating from the intestinal branch of the vagus during the previous stage.

It rapidly thins out posteriorly and also approaches closer and closer to the lateral line. At the front end of the trunk it is quite in contact with it, and a short way behind this region the cells of the lateral line arrange themselves in a gable-like form, in the angle of which the nerve is situated (Pl. XII.

fig. 3*b*, and 3*c*). In this position the nerve though small is still very distinct in all good sections, and is formed of a rod of protoplasm, with scattered nuclei, in which I could not detect a distinct indication of cell-areas. The hinder part of the nerve becomes continually smaller and smaller, without however presenting any indication of becoming fused with the epiblast, and eventually ceases to be visible some considerable distance in front of the posterior end of the lateral line.

The lateral line itself presents some points of not inconsiderable interest. In the first place, it is very narrow anteriorly and throughout the greater part of its length, but widens out at its hinder end, and is widest of all at its termination, which is perfectly abrupt. The following measurements of it were taken from an embryo belonging to stage L, which though not quite my second youngest embryo is only slightly older. At its hinder end it was 0·17 Mm. broad. At a point not far from this it was 0·09 Mm. broad, and anteriorly it was 0·05 Mm. broad. These measurements clearly show that the lateral line is broadest at what may be called its growing-point, a fact which explains its extraordinary breadth in the anterior part of the body at my first stage, viz. 0·28 Mm., a breadth which strangely contrasts with the breadth, viz. 0·05 Mm., which it has in the same part of the body at the present stage.

It still continues to form a linear area of modified epidermis, and has no segmental characters. Anteriorly it is formed by the cells of mucous layer becoming more columnar (Pl. XII. fig. 3*a*). In its middle region the cells of the mucous layer in it are still simply elongated, but, as has been said above, have a gable-like arrangement, so as partially to enclose the nerve (Pl. XII. fig. 3*b*). Nearer the hind end of the trunk a space appears in it between its columnar cells and the flattened cells of the outermost layer of the skin (Pl. XII. fig. 3*c*), and this space becomes posteriorly invested by a very definite layer of cells. The space (Pl. XII. fig. 3*d*) or lumen has a slit-like section, and is not formed by the closing in of an originally open groove, but by the formation of a cavity in the midst of the cells of the lateral line. Its walls are formed by a layer of columnar cells on the inner side, and flattened cells on the outer side, both layers however appearing to be derived from the mucous layer of the epidermis. The outer layer of cells attains its greatest thickness dorsally.

During stages M, N, O, the lateral nerve gradually passes inwards into the connective tissue between the dorso-lateral and the ventro-lateral muscles, and becomes even before the close of stage N completely isolated from the lateral line.

The growth of the lateral line itself remains for some time almost stationary; anteriorly the cells retain the gable-like arrangement which characterised them at an earlier period, but cease to enclose the nerve; posteriorly the line retains its original more complicated constitution as a closed canal. In stage O the cells of the anterior part of the line, as well as those of the posterior, commence to assume a tubular arrangement, and the lateral line takes the form of a canal. The tubular form is due to a hollowing out of the lateral line itself and a rearrangement of its cells. As the lateral line becomes converted into a canal it recedes from the surface.

In stage P the first indication of segmental apertures to the exterior make their appearance, vide Pl. XII. fig. 4. The lateral line forms a canal situated completely below the skin, but at intervals (corresponding with segments) sends upwards and outwards prolongations towards the exterior. These prolongations do not during stage P acquire external openings. As is shown in my figure, a special area of the inner border of the canal of the lateral line becomes distinguished by its structure from the remainder.

No account of the lateral line would be complete without some allusion to the similar sensory structures which have such a wide distribution on the heads of Elasmobranchs; and this is especially important in the present instance, owing to the light thrown by a study of their development on the origin of the nerves which supply the sense-organs of this class. The so-called mucous canals of the head originate in the same way as does the lateral line; they are products of the mucous layer of the epidermis. They eventually form either canals with numerous openings to the exterior, or isolated tubes with terminal ampulliform dilatations.

I have not definitely determined whether the canal-system of the head arises in connection with the lateral line, or only eventually becomes so connected. The important point to be noticed is, that at first no nervous structures are to be seen in connection with it. In stage O nerves for the mucous canals make their appearance as delicate branches of the main stems. These nerve-stems are very much ramified, and their branches have, in a large number of instances, an obvious tendency towards a particular sense-organ (Pl. XII. figs. 5 and 6).

I have not during stage O been able to detect a case of direct continuity between the two. This is, however, established in the succeeding stage P, in the case of the canals, and the facility with which it may be observed would probably render the embryo Elasmobranch a very favourable object for studying the connection between nerves and terminal sense-organs. The nerve (Pl. XII. fig. 7) dilates somewhat before uniting with the sense-organ, and the protoplasm of the nerve and the sense-organ become completely fused. The basement membrane of the skin is not continuous across their point of junction, and appears to unite with a delicate membrane-like structure, which invests the termination of the nerve. The ampullæ would seem to receive their nervous supply somewhat later than the canals, and the terminal swellings of the nerves supplying them are larger than in the case of the canals, and the connection between the ampullæ and the nerves not so clear. In the case of the head, there can for Elasmobranchs be hardly a question that the nerves which supply the mucous canals grow centrifugally from the original cranial nerve-stems, and do not originate in a peripheral manner from the integument.

This is an important point to make certain of in settling any doubtful features in the nervous supply of the lateral line. Professor Semper[1], with whom as dealing with Elasmobranchs we are more directly concerned, makes the following statement: "At the time when at the front end the lateral nerve has already completely separated itself from the ectoderm, and is situated amongst the muscles, it still lies in the middle of the body close to the ectoderm, and at the hind end of the body is not yet completely segmented off (abgegliedert) from the ectoderm." Although the last sentence of this quotation may seem to be opposed to my statements, yet it appears to me

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[1] *Loc. cit.* p. 398.

probable that Professor Semper has merely seen the lateral nerve partially enclosed in the ectoderm. This position of the nerve no doubt affords a *presumption, but only a presumption,* in favour of a direct origin of the lateral nerve from the ectoderm; but against this interpretation of it are the following facts:

(1) That the front part of the lateral line is undoubtedly supplied by branches which arise in the ordinary way from the intestinal branch of the vagus; and we should not expect to find part of the lateral line supplied by nerves which originate in one way, and the remainder supplied by a nerve having a completely different and abnormal mode of origin.

(2) The growth of the lateral line is quite independent of that of the lateral nerve: the latter arises subsequently to the lateral line, and, so far as is shown by the inconclusive observation of my earliest stage, as an offshoot from the intestinal branch of the vagus; and though it grows along at first in close contact with the lateral nerve, yet it never presents, so far as I have seen, any indubitable indication of becoming split off from this, or of fusing with it.

(3) The fact that the cranial representatives of the lateral line are supplied with nerves which originate in the normal way[1], affords a strong argument in favour of the lateral line receiving an ordinary nerve-supply.

Considering all these facts, I am led to the conclusion *that the lateral nerve in Elasmobranchs arises as a branch of the vagus, and not as a direct product of the external epiblast.*

An interesting feature about the lateral line and the similar cephalic structures, is the fact of these being the only sense organs in Elasmobranchs which originate entirely from the mucous layer of the epiblast. This, coupled with the well-known facts about the Amphibian epiblast, and the fact that the mucous canals are the only sense-organs which originate subsequently to the distinct differentiation of the epiblast into mucous and horny layers, goes far to prove[2] that the mucous layer

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[1] Götte extends his statements about the lateral nerve to the nerves supplying the mucous canals in the head; but my observations appear to me, as far as Elasmobranchs are concerned, nearly conclusive against such a derivation of the nerves in the head.

[2] I believe that Götte, amongst his very numerous valuable remarks in the *Entwicklungsgeschichte der Unke*, has put forward a view similar to this, though I cannot put my hand on the reference.

is to be regarded as the active layer of the epiblast, and that after this has become differentiated, an organ formed from the epiblast is always a product of it.

Muscle-Plates.

The muscle-plates at the close of stage K were flattened angular bodies with the apex directed forwards, their ventral edge being opposite the segmental duct, and their dorsal edge on a level with the middle of the spinal cord. They were composed of two layers, formed for the most part of columnar cells, but a small part of their splanchnic layer opposite the notochord had already become differentiated into longitudinal muscles.

During stage L the growth of these plates is very rapid, and their upper ends extend to the summit of the neural canal, and their lower ones nearly meet in the median ventral line. The original band of muscles (Pl. X. fig. 8 *m. p'*), whose growth was so slow during stages I and K, now increases with great rapidity, and forms the nucleus of the whole voluntary muscular system. It extends upwards and downwards by the continuous conversion of fresh cells of the splanchnic layer into muscle-cells. At the same time it grows rapidly in thickness, but it requires some little patience and care to unravel the details of this growth; and it will be necessary to enter on a slight digression as to the relations of the muscle-plates to the surrounding connective tissue.

As the muscle-plates grow dorsalwards and ventralwards their ends dive into the general connective tissue, whose origin has already been described (Pl. XII. fig. 1). At the same time the connective-tissue cells, which by this process become situated between the ends of the muscle-plates and the skin, grow upwards and downwards, and gradually form a complete layer separating the muscle-plates from the skin. The cells forming the ends of the muscle-plates retain unaltered their primitive undifferentiated character, and the separation between them and the surrounding connective-tissue cells is very marked. This however ceases to be the case in the parts of the muscle-plates on a level with the notochord and lower part of the medullary canal; the thinnest sections and most careful examination are needed to elucidate the changes taking place in this region. The cells which form the somatic layer of the muscle-plates then begin to elongate and become converted into muscle-cells, at the same time that they are increasing in number to meet the rapid demands upon them. One result of these changes is the loss of the original clearness in the external boundary between the muscle-plates and the adjoining connective-tissue cells, which is only in exceptional cases to be seen so distinctly as it may be in Pl. XII. fig. 1 and 8. Longitudinal horizontal sections are the most instructive for studying the growth of the muscles, but transverse sections are also needed. The interpretation of the transverse ones is however rendered difficult, both by rapid alterations in the thickness of the connective-tissue layer between the skin and the muscle-plates (shown in Pl. XII. fig. 8), and by the angular shape of the muscle-plates themselves.

A careful study of both longitudinal and transverse sections has enabled me to satisfy myself of the fact that the cells of the somatic layer of the protovertebræ, equally with the cells of the splanchnic layer, are converted into muscle-cells, and some of these are represented in the act of undergoing this conversion in Pl. XII. fig. 8; but the difficulty of distinguishing the outline of the somatic layer of the muscle-plates, at the time its cells become converted into muscle-cells, renders it very difficult to determine whether any cells of this layer join the surrounding connective tissue. General considerations certainly lead me to think that they do not; but my observations do not definitely settle the point.

From these facts it is clear, as was briefly stated in the last chapter, *that both layers of the muscle-plate are concerned in forming the great lateral muscle, though the splanchnic layer is converted into muscles very much sooner than the somatic*[1].

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[1] The difference between Dr Götte's account of the development of the muscles and my own consists mainly in my attributing to the somatic layer of the muscle-plates a share in the formation of the great lateral muscles, which he denies to it. In an earlier section of this Monograph, pp. 115, 116, too much stress was unintentionally laid on the divergence of our views; a divergence which appears to have, in part at least, arisen, not from our observations being opposed, but from Dr Götte's having taken the highly differentiated Bombinator as his type instead of the less differentiated Elasmobranch.

The remainder of the history of the muscle-plates presents no points of special interest.

Till the close of stage L, the muscle-plates are not distinctly divided into dorsal and ventral segments, but this division, which is so characteristic of the adult, commences to manifest itself during stage M, and is quite completed in the succeeding stage. It is effected by the appearance, nearly opposite the lateral line, of a layer of connective tissue which divides the muscles on each side into a dorso-lateral and ventro-lateral section. Even during stage O the ends of the muscle-plate are formed of undifferentiated columnar cells. The peculiar outlines of the intermuscular septa gradually appear during the later stages of development, causing the well-known appearances of the muscles in transverse sections, but require no special notice here.

With reference to the histological features of the development of the muscle-fibres, I have not pushed my investigations very far. The primitive cells present the ordinary division, well known since Remak, into a striated portion and a non-striated portion, and in the latter a nucleus is to be seen which soon undergoes division and gives rise to several nuclei in the non-striated part, while the striated part of each cell becomes divided up into a number of fibrillæ. I have not however determined what exact relation the original cells hold to the eventual primitive bundles, or anything with reference to the development of the sarcolemma.

The Muscles of the Limbs.—These are formed during stage O coincidently with the cartilaginous skeleton, in the form of two bands of longitudinal fibres on the dorsal and ventral surfaces of the limbs. Dr Kleinenberg first called my attention to the fact that he had proved the limb-muscles in *Lacerta* to be derived from the muscle-plates. This I at first believed did not hold good for Elasmobranchs, but have since determined that it does so. Between stages K and L the muscle-plates grow downwards as far as the limbs and then turn outwards and grow into them (Pl. XVII. fig. 1). Small portions of several muscle-plates come in this way to be situated in the limbs, and are very soon segmented off from the remainder of the muscle-plates. The portions of muscle-plates thus introduced into the limbs soon lose their original distinctness, and can no longer be recognised in stage L. There can however be but little doubt that they supply the tissue for the muscles of the limbs. The muscle-plates themselves after giving off these buds to the limbs grow downwards, and by stage L cease to show any trace of what has occurred (Pl. XII. fig. 1). This fact, coupled with the late development of the muscles of the limbs (stage O), caused me to fall into my original error.

The Vertebral Column and Notochord.

In the previous chapter (p. 107) an account was given of the origin of the tissue destined to form the vertebral bodies; it merely remains to describe the changes undergone by this in becoming converted into the permanent vertebræ.

This subject has already been dealt with by a considerable number of anatomists, and my investigations coincide in the main with the results of my predecessors. Especially the researches of Gegenbaur[1] may be singled out as containing the pith of the whole subject, and my results, while agreeing in all but minor points with his, do not supplement them to any very great extent. I cannot do more than confirm Götte's[2] account of the development of the hæmal arches, and may add that Cartier[3] has given a good account of the later development of the centra. Under the circumstances it has not appeared to me to be worth while recording with great detail my investigations; but I hope to be able to give a somewhat more complete history of the whole subject than has appeared in any single previous memoir.

At their first appearance the cells destined to form the permanent vertebræ present the same segmentation as the muscle-plates. This segmentation soon disappears, and between stages K and L the tissue of the vertebral column forms a continuous investment of the notochord which cannot be distinguished from the adjoining connective tissue. Immediately surrounding the notochord a layer formed of a single row of cells may be observed, which is not however very distinctly marked[4].

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[1] *Das Kopfskelet d. Selachier*, p. 123.

[2] *Entwicklungsgeschichte d. Unke*, p. 433-4.

[3] *Zeitschrift f. Wiss. Anat.* Bd. xxv., Supplement.

[4] Vide p. 138.

During the stage L there appear four special concentrations of mesoblastic tissue adjoining the notochord, two of them dorsal and two of them ventral. They are not segmented, and form four ridges seated on the sides of the notochord. They are united with each other by a delicate layer of tissue, and constitute the rudiments of the neural and hæmal arches. In longitudinal sections of stage L special concentrated wedge-shaped masses of tissue are to be seen between the muscle-plates, which must not be confused with these rudiments. Immediately around the notochord the delicate investment of cells previously mentioned, is still present.

The rudiments of the arches increase in size and distinctness in the succeeding stages, and by stage N have unquestionably assumed the constitution of embryonic cartilage. In the meantime there has appeared surrounding the sheath of the notochord a well-marked layer of tissue which stains deeply with hæmatoxylin, and with the highest power may be observed to contain flattened nuclei. It is barely thicker than the adjoining sheath, but is nevertheless the rudiment of vertebral bodies. Pl. XII. fig. 9, *vb*. Whence does this layer arise? To this question I cannot give a quite satisfactory answer. It is natural to conclude that it is derived from the previously existing mesoblastic investment of the notochord, but in the case of the vertebral column I have not been able to prove this. Observations on the base of the brain afford fairly conclusive evidence that the homologous tissue present there has this origin. Gegenbaur apparently answers the question of the origin of this layer in the way suggested above, and gives a figure in support of his conclusion (Pl. XXII. fig. 3)[1].

The layer of tissue which forms the vertebral bodies rapidly increases in thickness, and very soon, at a somewhat earlier period than represented in Gegenbaur's Plate XXII. fig. 4, a distinct membrane (Kölliker's Membrana Elastica Externa) may easily be recognised surrounding it and separating it

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[1] None of my specimens resembles this figure, and the layer when first formed is in my embryos much thinner than represented by Gegenbaur, and the histological structure of the embryonic cartilage is very different from that of the cartilage in the figures alluded to. Götte's very valuable researches with reference to the origin of this layer in Amphibians tend to confirm the view advocated in the text.

from the adjoining tissue of the arches. Gegenbaur's figure gives an excellent representation of the appearance of this layer at the period under consideration. It is formed of a homogeneous basis containing elongated concentrically arranged nuclei, and constitutes a uniform unsegmented investment for the notochord (vide Pl. XII. fig. 10).

The neural and hæmal arches now either cease altogether to be united with each other by a layer of embryonic cartilage, or else the layer uniting them is so delicate that it cannot be recognised as true cartilage. They have moreover by stage P undergone a series of important changes. The tissue of the neural arches does not any longer form a continuous sheet, but is divided into (1) a series of arches encircling the spinal cord, and (2) a basal portion resting on the cartilaginous sheath of the notochord. There are two arches to each muscle-plate, one continuous with the basal portion of the arch-tissue and forming the true arch, which springs opposite the centre of a vertebral body, and the second not so continuous, which forms what is usually known as the intercalated piece. Between every pair of true arches the two roots of a single spinal nerve pass out. The anterior root passes out in front of an intercalated piece and the posterior behind it[1].

The basal portion of the arch-tissue likewise undergoes differentiation into a vertebral part continuous with the true arch and formed of hyaline cartilage, and an intervertebral segment formed of a more fibrous tissue.

The hæmal arches, like the neural arches, become divided into a layer of tissue adjoining the cartilaginous sheath of the notochord, and processes springing out from this opposite the centres of the vertebræ. These processes throughout the region of the trunk in front of the anus pass into the space between the dorsal and ventral muscles, and are to be regarded as rudiments of ribs. The tissue with which they are continuous, which is exactly equivalent to the tissue from which the neural arches originate, is not truly a part of the rib. In the tail, behind the anus and kidneys, the cardinal

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[1] In the adult Scyllium it is well known that the posterior root pierces the intercalated cartilage and the anterior root the true neural arch. This however does not seem to be the case in the embryo at stage P.

veins fuse to form an impaired caudal vein below the aorta, and in this part a fresh series of processes originates on each side from the hæmal tissue adjoining the cartilaginous sheath of the notochord, and eventually, by the junction of the processes of the two sides, a canal which contains the aorta and caudal vein is formed below the notochord. These processes for a few segments coexist with small ribs (vide Pl. XII. fig. 10), a fact which shows (1) that they cannot be regarded as modified ribs, and (2) that the tissue from which they spring is to be viewed as a kind of general basis for all the hæmal processes which may arise, and is not specially connected with any one set of processes.

While these changes (all of which are effected during stage P) are taking place in the arches, the tissue of the vertebral bodies or cartilaginous investment of the notochord, though much thicker than before, still remains as a continuous tube whose wall exhibits no segmental differentiations.

It is in stage Q that these differentiations first appear in the vertebral regions opposite the origin of the neural arches. The outermost part of the cartilage at these points becomes hyaline and almost undistinguishable in structure from the tissue of the arches[1]. These patches of hyaline cartilage grow larger and cause the vertebral parts of the column to constrict the notochord, whilst the intervertebral parts remain more passive, but become composed of cells with very little intercellular substance. Coincidently also with these changes, part of the layer internal to the hyaline cartilage becomes modified to form a somewhat peculiar tissue, the intercellular substance of which does not stain, and in which calcification eventually arises (Pl. XII. fig. 11). The innermost layer adjoining the notochord retains its primitive fibrous character, and is distinguishable as a separate layer through both the vertebral and the intervertebral regions. As a result of these changes a transverse section through the centre of the vertebral regions now exhibits three successive rings (vide Pl. XII. fig. 11), an external ring of hyaline cartilage invested by 'the membrana elastica externa' (*m.el*), followed by a

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[1] A good representation of a longitudinal section at this stage is given by Cartier (*Zeitschrift f. Wiss. Zoologie*, Bd. XXV., Supplement Pl. IV. fig. 1), who also gives a fair description of the succeeding changes of the vertebral column.

ring of calcifying cartilage, and internal to this a ring of fibrous cartilage, which adjoins the now slightly constricted notochord. A transverse section of an intervertebral region shows only a thick outer and thin inner ring of fibrous cartilage, the latter in contact with the sheath of the unconstricted notochord.

The constriction of the notochord proceeds till in the centre of the vertebræ it merely forms a fibrous band. The tissue internal to the calcifying cartilage then becomes hyaline, so that there is formed in the centre of each vertebral body a ring of hyaline cartilage immediately surrounding the fibrous band which connects the two unconstricted segments of the notochord. The intervertebral tissue becomes more and more fibrous. In Cartier's paper before quoted there is a figure (fig. 3) which represents the appearance presented by a longitudinal section of the vertebral column at this stage.

The relation of the vertebral bodies to the arches requires a short notice. The vertebral hyaline cartilage becomes almost precisely similar to the tissue of the arches, and the result is, that were it not for the 'membrana elastica externa' it would be hardly possible to distinguish the limits of the two tissues. This membrane however persists till the hyaline cartilage has become a very thick layer (Pl. XII. fig. 11), but I have failed to detect it in the adult, so that I cannot there clearly distinguish the arches from the body of the vertebræ. From a comparison however of the adult with the embryo, it is clear that the arches at most form but a small part of what is usually spoken of as the body of the vertebræ.

The changes in the notochord itself during the stages subsequent to K are not of great importance. The central part retains for some time its previous structure, being formed of large vacuolated cells with an occasional triangular patch of protoplasm containing the starved nucleus and invested by indurated layers of protoplasm. These indurated layers are all fused, and are probably rightly regarded by Gegenbaur and Götte as representing a sparse intercellular matter. The external protoplasmic layer of the notochord ceases shortly after stage K to exhibit any traces of a division into separate cells, but forms a continuous layer with irregular prominences and numerous nuclei (Pl. XII. fig. 9). In the stages subsequent to P further changes take place in the notochord: the remains of the cells become more scanty and the intercellular tissue assumes a radiating arrangement, giving to sections of the notochord the appearance of a number of lines radiating from the centre to the periphery (Pl. XII. fig. 11).

The sheath of the notochord at first grows in thickness, and during stage L there is no difficulty in seeing in it the fine radial markings already noticed by Müller[1] and Gegenbaur[2], and regarded by them as indicating pores. Closely investing the sheath of the notochord there is to be seen a distinct membrane, which, though as a rule closely adherent to the sheath, in some examples separates itself from it. It is perhaps the membrane identified by W. Müller[3] (though not by Gegenbaur) as Kölliker's 'membrana elastica interna.' After the formation of the cartilaginous investment of the notochord, this membrane becomes more difficult to see than in the earlier stage, though I still fancy that I have been able to detect it. The sheath of notochord also appears to me to become thinner, and its radial striation is certainly less easy to detect[4].

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[1] *Jenaische Zeitschrift*, Vol. VI. [2] *Loc. cit.* [3] *Loc. cit.*

[4] Gegenbaur makes the reserve statement with reference to the sheath of the notochord. For my own sections the statement in the text certainly holds good. Fortunately the point is one of no importance.

CHAPTER VIII.

DEVELOPMENT OF THE SPINAL NERVES AND OF THE SYMPATHETIC NERVOUS SYSTEM.

The spinal nerves.

THE development of the spinal nerves has been already treated by me at considerable length in a paper read before the Royal Society in December, 1875[1], and I have but little fresh matter to add to the facts narrated in that paper. The succeeding account, though fairly complete, is much less full than the previous one in the *Philosophical Transactions*, but a number of morphological considerations bearing on this subject are discussed.

The rudiments of the posterior roots make their appearance considerably before those of the anterior roots. They arise during stage I, as outgrowths from the spinal cord, at a time when the muscle-plates do not extend beyond a third of the way up the sides of the spinal cord, and in a part where no scattered mesoblast-cells are present. They are formed first in the anterior part of the body and successively in the posterior parts, in the following way. At a point where a spinal nerve is about to arise, the cells of the dorsal part of the cord begin to proliferate, and the uniform outline of the cord becomes broken (Pl. XIII. fig. 3). There is formed in this way a small prominence of cells springing from the summit of the spinal cord, and constituting a rudiment of a pair of posterior roots. In sections anterior to the point where a nerve is about to appear, the nerve-rudiments are always very distinctly formed. Such a section is shown in Pl. XIII. fig. 2, and the rudiments may there be seen as two club-shaped masses of cells, which have grown outwards and downwards from the extreme dorsal summit of the neural canal and in contact with its walls. The rudiments of the two sides meet at their point of origin at the dorsal median line, and are dorsally perfectly continuous with the walls of the canal.

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[1] *Phil. Trans.* Vol. 166, p. 175.

It is a remarkable fact that rudiments of posterior roots are to be seen in every section. This may be interpreted as meaning that the rudiments are in very close contact with each other, but more probably means, as I hope to show in the sequel, that there arises from the spinal cord a continuous outgrowth from which discontinuous processes (the rudiments of posterior roots) grow out.

After their first formation these rudiments grow rapidly ventralwards in close contact with the spinal cord (vide Pl. XIII. fig. 1, and Pl. X. figs. 6 and 7), but soon meet with and become partially enclosed in the mesoblastic tissue (Pl. X. fig. 7). The similarity of the mesoblast and nerve-tissue in Scyllium and Pristiurus embryos hardened in picric or chromic acid, render the nerves in these genera, at the stage when they first become enveloped in mesoblast, difficult objects to observe; but no similar difficulty is encountered in the case of Torpedo embryos.

While the rudiments of the posterior roots are still quite short, those of the anterior roots make their first appearance. Each of these (Pl. XIII. fig. 4 *a.r.*) arises as a very small but distinct conical outgrowth from a ventral corner of the spinal cord. From the very first the rudiments of the anterior roots have an indistinct form of peripheral termination and somewhat fibrous appearance, while the protoplasm of which they are composed becomes attenuated towards its end. The points of origin of the anterior roots from the spinal cord are separated by considerable intervals. In this fact, and also in the fact of the nerves of the two sides never being united with each other in the median line, the anterior roots exhibit a marked contrast to the posterior. There are thus constituted, before the close of stage I, the rudiments of both the anterior and posterior roots of the spinal nerves. The rudiments of both of these take their origin from the involuted epiblast of the neural canal, and the two roots of each spinal nerve are at first quite unconnected with each other. It is scarcely necessary to state that the pairs of roots correspond in number with the muscle-plates.

It is not my intention to enter with any detail into the subsequent changes of the rudiments whose origin has been described, but a few points especially connected with their early development are sufficiently important to call for attention.

One feature of the posterior roots at their first formation is the fact that they appear as processes of a continuous outgrowth of the spinal cord. This state of affairs is not of long continuance, and before the close of stage I each posterior root has a separate junction with the spinal cord. What then becomes of the originally continuous outgrowth? It has not been possible for me to trace the fate of this step by step; but the discovery that at a slightly later period (stage K) there is present a continuous commissure independent of the spinal cord connecting the dorsal and central extremities of all the spinal nerves, renders it very probable that the original continuous outgrowth becomes converted into this commissure. Like all the other nervous structures, this commissure is far more easily seen in embryos hardened in a mixture of osmic and chromic acids or osmic acid, than in those hardened in picric acid. Its existence must be regarded as one of the most remarkable results of my researches upon the Elasmobranch nervous system. At stage K it is fairly thick, though it becomes much thinner at a slightly later period. Its condition during stage K is shown in Plate XI. fig. 18, *com.* What it has been possible for me to make out of its eventual fate is mentioned subsequently[1].

A second feature of the earliest condition of the posterior roots is their attachment to the extreme dorsal summit of the spinal cord—a point of attachment very different from that which they eventually acquire. Before the commencement of stage K this state of things has become altered; and the posterior roots spring from the spinal cord in the position normal for Vertebrates.

This apparent migration caused me at first great perplexity, and I do not feel quite satisfied that I have yet got completely to the bottom of its meaning. The explanation which appears to me most probable has suggested itself in the course of some observations on the development of the thin roof of the fourth

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[1] It is not by any means always possible to detect this commissure in transverse sections. As I have suggested, in connection with a similar commissure connecting the vagus branches, it perhaps easily falls out of the section, and is always so small that the hole left would certainly be invisible.

ventricle. A growth of cells appears to take place in the median dorsal line of the roof of the spinal cord. This growth tends to divaricate the two lateral parts of the cord, which are originally contiguous in the dorsal line, and causes therefore the posterior roots, which at first spring from the dorsal summit, to assume an apparent attachment to the side of the cord at some little distance from the summit. If this is the true explanation of the change of position which takes place, it must be regarded as due rather to peculiar growths in the spinal cord, than to any alteration in the absolute attachment of the nerves.

By stage K the rudiment of the posterior root has become greatly elongated, and exhibits a division into three distinct portions (Pl. XIII. fig. 6):

(1) A proximal portion, in which is situated the pedicle of attachment to the wall of the neural canal.

(2) an enlarged portion, which may conveniently from its future fate be called the spinal ganglion.

(3) a distal portion beyond this.

The proximal portion presents a fairly uniform diameter, and ends dorsally in a rounded expansion; it is attached, remarkably enough, *not by its extremity, but by its side, to the spinal cord. The dorsal extremities of the posterior roots are therefore free.* It seems almost certain that the free dorsal extremities of these roots serve as the starting points for the dorsal commissure before mentioned, which connects the roots together. The attachment of the posterior nerve-root to the spinal cord is, on account of its small size, very difficult to observe. In favourable specimens there may however be seen a distinct cellular prominence from the spinal cord, which becomes continuous with a small prominence on the lateral border of the nerve-root near its distal extremity. The proximal extremity of the rudiment is composed of cells, which, by their small size and circular form, are easily distinguished from those which form the succeeding or ganglionic portion of the nerve. This succeeding part has a swollen configuration, and is composed of large elongated cells with oval nuclei. The remainder of the rudiment forms the commencement of the true nerve.

The anterior root, which, at the close of stage I, formed a small and inconspicuous prominence from the spinal cord, grows rapidly during the succeeding stages, and soon forms an elongated cellular structure with a wide attachment to the spinal cord (Pl. XIII. fig. 5). At first it passes obliquely and nearly horizontally outwards, but, before reaching the muscle-plate of its side, takes a bend downwards (Pl. XIII. fig. 7).

I have not definitely made out when the anterior and posterior roots unite, but this may easily be seen to take place before the close of stage K (Pl. XI. fig. 18).

One feature of some interest with reference to the anterior roots, is the fact that they arise not vertically below, but alternately with the dorsal roots, a condition which persists in the adult.

Although I have made some efforts to determine the eventual fate of the commissure uniting the dorsal roots, these have not hitherto been crowned with success. It grows thinner and thinner, becoming at the same time composed of fibrous protoplasm with imbedded nuclei (Pl. XIII. fig. 8 and 9). By stage M it is so small as to be quite indistinguishable in transverse sections ; and I have failed in stage P to recognize it at all. I can only conclude that it gradually atrophies, and finally vanishes without leaving a trace. Both its appearance and history are very remarkable, and deserve the careful attention of future investigators.

There can be little doubt that it is some sort of remnant of an ancestral structure in the nervous system; and it would appear to indicate that the central nervous system must originally have been formed of a median and two lateral strands. At the same time I very much doubt whether it can be brought into relation with the three rows of ganglion-cells (a median and two lateral) which are so frequently present on the ventral side of annelidan nerve-cords.

My results may be summarised as follows:—Along the extreme dorsal summit of the spinal cord there arises on each side a continuous outgrowth. From each outgrowth processes corresponding in number to the muscle-plates grow downwards. These are the rudiments of the posterior nerve-roots. The outgrowths, though at first attached to the spinal cord throughout their whole length, soon cease to be so, and remain in connection with it at certain points only, which form the primitive junctions of the posterior roots with the spinal cord. The original outgrowth on each side remains as a bridge, uniting together the dorsal extremities of all the posterior roots. The posterior roots, though primitively attached to the dorsal summit of the spinal cord, eventually come to arise from its sides. The original homogeneous rudiments before the close of stage K become differentiated into a root, a ganglion, and a nerve.

The anterior roots, like the posterior, are outgrowths from the spinal cord, but are united independently with it, and the points from which they spring originally, remain as those by which they are permanently attached. The anterior roots arise, not vertically below, but in the intervals between the posterior roots. They are at first quite separate from the posterior roots; but before the close of stage K a junction is effected between each posterior root and the corresponding anterior root. The anterior root joins the posterior at some little distance below its ganglion.

The results here arrived at are nearly in direct opposition to those of the majority of investigators, though in accordance, at least so far as the posterior roots are concerned, with the beautiful observations of Hensen 'on the Development of Mammalia[1].'

Mr Marshall[2] has more recently published a paper on the development of the nerves in Birds, in which he shows in a most striking manner that the observations recorded here for Elasmobranchs hold good for the posterior roots of Birds. The similarity between his figures and my own is very noticeable. A further discussion of the literature would be quite unprofitable, and I proceed at once to certain considerations suggested by the above observations.

General considerations.—One point of general anatomy upon which my observations throw considerable light, is the *primitive origin of nerves.* So long as it was admitted that the spinal and cerebral nerves developed in the embryo independently of the central nervous system, their mode of origin always presented to my mind considerable difficulties. It never ap-

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[1] *Zeit. f. Anat. u. Entwicklungsgeschichte*, Vol. I.

[2] *Journal of Anatomy and Physiology*, Vol. XI. April, 1877.

peared clear how it was possible for a state of things to have arisen in which the central nervous system as well as the peripheral terminations of nerves, whether motor or sensory, were formed independently of each other; while between them a third structure was developed, which, growing out either towards the centre or towards the periphery, ultimately brought the two into connection. That such a condition could be a primitive one seemed scarcely possible.

Still more remarkable did it appear, on the supposition that the primitive mode of formation of these parts was represented in the developmental history of Vertebrates, that we should find similar structural elements in the central and in the peripheral nervous systems. The central nervous system arises from the epiblast, and yet contains precisely similar nerve-cells and nerve-fibres to the peripheral nervous system, which, when derived from the mesoblast, was necessarily supposed to have an origin completely different from that of the central nervous system. Both of these difficulties are to a great extent removed by the facts of the development of these parts in Elasmobranchs.

It is possible to suppose that in their primitive differentiation contractile and sensory systems may, as in Hydra[1], have been developed from the protoplasm of even the same cell. As the sensory and motor systems became more complicated, the sensory portion of a cell would become separated by an increasing interval from the muscular part of a cell, and the two parts of a cell would only be connected by a long protoplasmic process. When such a condition as that was reached, the sensory portion of the cell would be called a ganglion-cell or terminal sensory organ, the connecting process a nerve, and the contractile portion of the cell a muscle-cell. When these organs were in this condition, it might not impossibly happen for the general developmental growth which tended to separate the ganglion-cell and the muscle-cell to be so rapid as to render it impossible for the growth of the connecting nerve to keep pace with it, and that thus the process connecting the ganglion-cell and the muscle-cell might become ruptured. Nevertheless the tendency of the process to grow from the ganglion cell to the

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[1] Kleinenberg Hydra.

muscle-cell, would remain, and when the rapid developmental growth had ceased, the two would become united again by the growth of the process which had previously been ruptured. It will be seen that this hypothesis, which I have considered only with reference to a single nerve and muscle-cell, might be extended so as to apply to a complicated central nervous system and peripheral nerves and muscles, and also could apply equally as well to the sensory as to the motor terminations of a nerve. In the case of the sensory termination, we should only have to suppose that the centre nervous cell became more and more separated by the general growth from the recipient terminal sensory cell, and that during the general growth the connection between the two was mechanically ruptured but restored again on the termination of the more rapid growth.

As the descendants of the animal in which the rupture occurred became progressively more complicated, the two terminal cells must have become widely separated at a continually earlier period, till finally they may have been separated at a period of development when they were indistinguishable from the surrounding embryonic cells; and since the rupture would also occur at this period, the primitive junction between the nerve-centre and termination would escape detection. The object of this hypothesis is to explain the facts, so far as they are known, of the development of the nervous system in Vertebrates.

In Vertebrates we certainly appear to have an outgrowth from the nervous system, which eventually becomes united with the muscle or sensory terminal organs. The ingenious hypothetical scheme of development of the nerves given by Hensen[1] would be far preferable to the one suggested if it could be brought into conformity with the facts. There is, however, at present no evidence for Hensen's view, as he himself admits, but considering how little we know of the finer details of the development of nerves, it seems not impossible that such evidence may be eventually forthcoming. The evidence from my own observation is, so far as it goes, against it. At a time anterior to the outgrowth of the spinal

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[1] Virchow's *Archiv*, Vol. XXXI. 1864.

nerves, I have shewn[1] that the spinal cord is completely invested by a delicate hyaline membrane. It is difficult to believe that this is pierced by a number of fine processes, which completely escape detection, but which must, nevertheless, be present on the hypothesis of Hensen.

The facts of the development of nerves in Vertebrates are unquestionably still involved in considerable doubt. It may, I think, be considered as certain, that in Elasmobranchs the roots of the spinal and cranial nerves are outgrowths of the central nervous system. How the final terminations of the nerves are formed is, however, far from being settled. Götte[2], whose account of the development of the spinal ganglia is completely in accordance with the ordinary views, yet states[3] that the growth of the nerve-fibres themselves is a centrifugal one from the ganglia. My own investigations prove that the ganglia have a centrifugal development, and also appear to demonstrate that the nerves themselves near the ganglion have a similar manner of growth. Moreover, the account given in the preceding chapter of the manner in which the nerves become connected with the mucous canals of the head, goes far to prove that the whole growth of the nerves is a centrifugal one. The combination of all these converging observations tells strongly in favour of this view.

On the other hand, Calberla[4] believes that in the tails of larval Amphibians he has seen connective-tissue cells unite with nerve-processes, and become converted into nerves, but he admits that he cannot definitely prove that the axis-cylinder has not a centrifugal growth, while the connective-tissue cells merely become converted into the sheath of the nerve. If Calberla's view be adopted, that the nerves are developed directly out of a chain of originally indifferent cells, each cell of the chain being converted in turn into a section of the nerve, an altogether different origin of nerves from that I have just suggested would seem to be indicated.

The obvious difficulty, already alluded to, of understanding how it is, according to the generally accepted mode of development of the spinal nerves, that precisely similar nerve-cells and

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[1] *Phil. Trans.*, 1876.

[2] *Entwicklungsgeschichte der Unke.*

[3] *Loc. cit.* p. 516.

[4] *Archiv für Micros. Anat.* Vol. XI. 1875.

nerves should arise in structures which have such different origins as the central nervous system and the spinal nerves, is completely removed if my statements on the development of the nerves in Elasmobranch represent the truth.

One point brought out in my investigations appears to me to have bearings upon the origin of the central canal of the vertebrate nervous system, and in consequence upon the origin of the vertebrate nervous system itself. This point is, that the posterior nerve-rudiments make their first appearance at the extreme dorsal summit of the spinal cord. The transverse section of the ventral nervous cord of an ordinary segmented Annelid consists of two symmetrical halves placed side by side. If by a mechanical folding the two lateral halves of the nervous cord became bent towards each other, while into the groove between the two the external skin became pushed, we should have an approximation to the vertebrate nervous system. Such a folding as this might take place to give extra rigidity to the body in the absence of a vertebral column.

If this folding were then completed in such a way that the groove, lined by external skin and situated between the two lateral columns of the nervous system, became converted into a canal, above and below which the two columns of the nervous system united, we should have in the transformed nervous cord an organ strongly resembling the spinal cord of Vertebrates.

It is well known that the nerve-cells are always situated on the ventral side of the abdominal nerve-cord of Annelids, either as a continuous layer, or in the form of two, or more usually, three bands. The dorsal side of the cord is composed of nerve-fibres or white matter. If the folding I have supposed were to take place in the Annelid nervous-cord, the grey and white matters would have very nearly the same relative situations as they have in the Vertebrate spinal cord. The grey matter would be situated in the interior and line the central canal, and the white matter would nearly surround the grey. The nerves would then arise, not from the sides of the nervous cord as in existing Annelids, but from its extreme ventral summit. One of the most striking features which I have brought to light with reference to the development of the posterior roots, is the fact of their growing out from the extreme dorsal summit of the neural canal, a position analogous to the ventral summit of the Annelidan nervous cord. Thus the posterior roots of the nerves in Elasmobranchs[1] arise, in the exact manner which might have been anticipated, were the spinal canal due to such a folding as I have suggested.

The argument from the position of the outgrowth of nerves becomes the more striking from its great peculiarity, and forms a feature which would be most perplexing without some such explanation as I have proposed. The central epithelium of the neural canal, according to this view, represents the external skin, and its ciliation in certain cases may, perhaps, be explained as a remnant of the ciliation of the external skin still found amongst many of the lower Annelids.

I have employed the comparison of the Vertebrate and Annelidan nervous cords, not so much to prove a genetic relation between the two, as to show the *à priori* possibility of the formation of a spinal cord, and the *à posteriori* evidence we have of the vertebrate canal having been formed in the way indicated. I have not made use of what is really my strongest argument, viz. that the embryological mode of formation of the spinal canal by a folding in of the external epiblast is the very method by which I supposed the spinal canal to have been formed in the ancestors of Vertebrates. My object has been to suggest a meaning for the peculiar primitive position of the posterior roots, rather than to attempt to explain in full the origin of the spinal canal.

Although the homologies between the Vertebrate and the Annelidan nervous systems are not necessarily involved in the questions which arise with reference to the formation of the spinal canal, they have nevertheless considerable bearings on it.

Two views have recently been put forward on this subject. Professor Gegenbaur[2] looks upon the central nervous system of Vertebrates as equivalent to the superior œsophageal ganglia

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[1] There are strong reasons for regarding the posterior roots as the primitive ones. These are spoken of later, but I may state that they depend:

(1) On the fact that only *posterior* roots exist in the brain.
(2) That only posterior roots exist in Amphioxus.
(3) That the posterior roots develope at an earlier period than the anterior.

[2] *Grundriss d. Vergleichenden Anat.* p. 264.

of Annelids and Arthropods only, while Professors Leydig[1] and Semper[2] and Dr Dohrn[3] compare it with the whole Annelidan nervous system.

The first of these two views is only possible on the supposition that Vertebrates are descended from unsegmented ancestors, and even then presents considerable difficulties. If the ancestors of Vertebrates were segmented animals, and several of the recent researches tend to shew that they were, they must almost certainly have possessed a nervous cord like that of existing Annelids. If such were the case, it is almost inconceivable that the greater portion of the nervous system which forms the ventral cord can have become lost, and the system reduced to the superior œsophageal ganglia. Dr Dohrn[4], who has speculated very profoundly on this matter, has attempted to explain and remove some of the difficulties which arise in comparing the nervous systems of Vertebrates and Annelids. He supposes that the segmented Annelids, from which Vertebrates are descended, were swimming animals. He further supposes that their alimentary canal was pierced by a number of gill-slits, and that the anterior amongst these served for the introduction of nutriment into the alimentary canal, in fact as supplementary mouths as well as for respiration. Eventually the old mouth and throat atrophied, and one pair of coalesced gill-slits came to serve as the sole mouth. Thus it came about that on the disappearance of that portion of the alimentary canal, which penetrated the œsophageal nervous ring, the latter structure ceased to be visible as such, and no part of the alimentary canal was any longer enclosed by a commissure of the central nervous system. With the change of mouth Dr Dohrn also supposes that there took place a change, which would for a swimming animal be one of no great difficulty, of the ventral for

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[1] *Bau des thierischen Körpers.*

[2] *Stammesverwandschaft d. Wirbelthiere u. Wirbellosen* and *Die Verwandschaftsbeziehungen d. gegliederten Thiere.* This latter work, for a copy of which I return my best thanks to the author, came into my hands after what follows was written, and I much regret only to have been able to make one or two passing allusions to it. The work is a most important contribution to the questions about to be discussed, and contains a great deal that is very suggestive; some of the conclusions with reference to the Nervous System appear to me however to be directly opposed to the observations on Spinal Nerves above recorded.

[3] *Ursprung d. Wirbelthiere u. Princip des Functionswechsels.*

[4] *Loc. cit.*

the dorsal surface. This general explanation of Dr Dohrn's, apart from the considerable difficulty of the fresh mouth, appears to me to be fairly satisfactory. Dr Dohrn has not however in my opinion satisfactorily dealt with the questions of detail which arise in connection with this comparison. One of the most important points for his theory is to settle the position where the nervous system was formerly pierced by the œsophagus. This position he fixes in the fourth ventricle, and supports his hypothesis by the thinness of the roof of the spinal canal in this place, and the absence (?) of nervous structures in it.

It appears to me that this thinness cannot be used as an argument. In the first place, if the hypothesis I have suggested as to the formation of the spinal canal be accepted, the formation of the canal must be supposed to have occurred in point of time either after or before the loss of the primitive mouth. If, on the one hand, the spinal canal made its appearance before the atrophy of the primitive mouth, the folding to form it must necessarily have ceased behind the mouth; and, on the supposition of the œsophageal ring having been situated in the region of the fourth ventricle, a continuation of the spinal canal could not be present in front of this part. If, on the other hand, the cerebro-spinal canal appeared after the disappearance of the primitive mouth, its roof must necessarily also be a formation subsequent to the atrophy of the mouth, and varieties of structure in it can have no bearing upon the previous position of the mouth.

But apart from speculations upon the origin of the spinal cord, there are strong arguments against Dr Dohrn's view about the fourth ventricle. In the first place, were the fourth ventricle to be the part of the nervous system which previously formed the œsophageal commissures, we should expect to find the opening in the nervous system at this point to be visible at an early period of development, and at a later period to cease to be so. The reverse is however the case. In early embryonic life the roof of the fourth ventricle is indistinguishable from other parts of the nervous system, and only thins out at a later period. Further than this, any explanation of the thin roof of the fourth ventricle ought also to elucidate the nearly similar structure in the sinus rhomboidalis, and cannot be considered satisfactory unless it does so.

The peculiarities of the cerebro-spinal canal in the region of the brain appear to me to present considerable difficulties in the way of comparing the central nervous system of Vertebrates and segmented Annelids. The manner in which the cerebro-spinal canal is prolonged into the optic vesicles, the cerebral and the optic lobes is certainly opposed both to an intelligible explanation of the spinal canal itself, and also to a comparison of the two nervous systems under consideration.

Its continuation into the cerebral hemispheres and into the optic lobes (mid-brain) may perhaps be looked upon as due to peculiar secondary growths of those two ganglia, but it is very difficult to understand its continuation into the optic vesicles.

If it be granted that the spinal canal has arisen from a folding in of the external skin, then the present inner surface of the optic vesicle must also have been its original outer surface, and it follows as a necessary consequence that the present position of the rods and cones behind and not in front of the nervous structures of the retina was not the primitive one. The rods and cones arise, as is well known, from the inner surface of the outer portion of the optic vesicle, and must, according to the above view, be supposed originally to have been situated on the external surface, and have only come to occupy their present position during the folding in, which resulted in the spinal canal. On *à priori* grounds we should certainly expect the rods and cones to have resulted from the differentiation of a layer of cells external to the conducting nervous structures. The position of the rods and cones posterior to these suggests therefore that some peculiar infolding has occurred, and may be used as an argument to prove that the medullary groove is no mere embryonic structure, but the embryonic repetition of an ancestral change. The supposition of such a change of position in the rods and cones necessarily implies that the folding in to form the spinal canal must have been a very slow one. It must have given time to the refracting media of the eye gradually to travel round, so as still to maintain their primitive position, while in successive generations a rudimentary spinal furrow carrying with it the retina became gradually converted into a canal[1].

If Dr Dohrn's comparison of the vertebrate nervous system with that of segmented Annelids be accepted, the following two points must in my opinion be admitted:—

(1) That the formation of the cerebro-spinal canal was subsequent to the loss of the old mouth.

(2) That the position of the old mouth is still unknown.

The well-known view of looking at the pituitary and pineal growths as the remnants of the primitive œsophagus, has no doubt some features to recommend it. Nearly conclusive against it is the fact that the pituitary involution is not, as used to be supposed, a growth towards the infundibulum of the hypoblast of the œsophagus, but of the epiblast of the mouth. It is almost inconceivable that an involution from the present mouth can have assisted in forming part of the old œsophagus.

There is a view not involving the difficulty of the œsophageal ring, fresh mouth[2], and of the change of the ventral to the dorsal surface, which, though so far unsupported by any

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[1] Professor Huxley informs me that he has for many years entertained somewhat similar views to those in the text about the position of the rods and cones, and has been accustomed to teach them in his lectures.

[2] Professor Semper (*Die Verwandtschaftsbeziehungen d. gegliederten Thiere, Arbeiten aus d. Zool.-zoot. Institut*, Würzburg, 1876) has some interesting speculations on the difficult question of the vertebrate mouth, which have unfortunately come to my knowledge too late to be either fully discussed or incorporated in the text. These speculations are founded on a comparison of the condition of the mouth in Turbellarians and Nemertines. He comes to the conclusion that there was a primitive mouth on the cardiac side of the supra-œsophageal ganglion, which is the existing mouth of Turbellarians and Vertebrates and the opening of the proboscis of Nemertines, but which has been replaced by a fresh mouth on the neural side in Annelids and Nemertines. In Nemertines however the two mouths co exist—the vertebrate mouth as the opening of the proboscis, and the Annelid mouth as the opening for the alimentary tract. This ingenious hypothesis is supported by certain anatomical facts, which do not appear to me of great weight, but for which the reader must refer to the original paper. It no doubt avoids the difficulty of the present position of the vertebrate mouth, but unfortunately at the same time substitutes an equal difficulty in the origin of the Annelidan mouth. This Professor Semper attempts to get over by an hypothesis which to my mind is not very satisfactory (p. 378), which, however, and this Professor Semper does not appear to have noticed, *could equally well be employed to explain the origin of a Vertebrate mouth as a secondary formation subsequent to the Annelidan mouth.* Under these circumstances this fresh hypothesis does not bring us very much nearer to a solution of the vertebrate-annelid mouth question, but merely substitutes one difficulty for another; and does not appear to me so satisfactory as the hypothesis suggested in the text.

At the same time Professor Semper's hypothesis suggests an explanation of that curious organ the Nemertine proboscis. If the order of changes firm basis of observed facts, nevertheless appears to me worth suggesting. It assumes that Vertebrates are descended *not* through the present line of segmented Vermes, but through some other line which has now, so far as is known, completely vanished. This line must be supposed to have originated from the same *unsegmented Vermes* as the present segmented Annelids. They therefore acquired fundamentally similar segmental and other Annelidan organs.

The difference between the two branches of the Vermes lay in the nervous system. The unsegmented ancestors of the *present* Annelids seem to have had a pair of super-œsophageal ganglia, from which two main nervous stems extended backwards, one on each side of the body. Such a nervous system in fact as is possessed by existing Nemertines or Turbellarians[1]. As the Vermes became segmented and formed the Annelids, these side nerves seem to have developed ganglia, corresponding in number with the segments, and finally, approximating on the ventral surface, to have formed the ventral cord[2].

The other branch of Vermes which I suppose to have been the ancestors of Vertebrates started from the same stock as existing Annelids, but I conceive the lateral nerve-cords, instead of approximating ventrally, to have done so dorsally, and thus a dorsal cord to have become formed analogous to the ventral cord of living Annelids, only without an œsophageal nerve-ring[3].

It appears to me, (if the difficulties of comparing the Annelidan ventral cord with the spinal cord of Vertebrates are found to be insurmountable), that this hypothesis would involve far fewer improbabilities than one which supposes the whole central nervous system of Vertebrates to be homologous with the super-œsophageal ganglia. The mode of formation of a

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suggested by him were altered it might be possible to suppose that there never was more than one mouth for all Vermes, but that the proboscis in Nemertines gradually split itself off from the œsophagus to which it originally belonged, and became quite free and provided with a separate opening and perhaps carried with it the so-called vagus of Professors Semper and Leydig.

[1] It is not of course to be supposed that the primitive nervous system was pierced by a proboscis like that of the Nemertines.

[2] This is Gegenbaur's view of the development of the ventral cord, and I regard it in the meantime as the most probable view which has been suggested.

[3] A dorsal instead of a ventral approximation of the lateral nerve-cords would be possible in the descendants of such living segmented Vermes as Saccocirrus and Polygordius.

nervous system presupposed in my hypothesis, well accords with what we know of the formation of the ventral cord in existing Annelids.

The supposition of the existence of another branch of segmented Vermes is not a very great difficulty. Even at the present day we have possibly more than one branch of Vermes which have independently acquired segmentation, viz.: the Chœtopodous Annelids and the Hirudinea. If the latter is an isolated branch, it is especially interesting from having independently developed a series of segmental organs like those of Chœtopodous Annelids, which we must suppose the ancestors of Vertebrates also to have done if they too form an independent branch.

In addition to the difficulty of imagining a fresh line of segmented Vermes, there is another difficulty to my view, viz.: the fact that in almost all Vermes, the blood flows forwards in the dorsal vessel, and backwards in the ventral vessel. This condition of the circulation very well suits the view of a change of the dorsal for the ventral surfaces, but is opposed to these surfaces being the same for Vertebrates and Vermes. I cannot however regard this point as a very serious difficulty to my view, considering how undefined is the circulation in the unsegmented groups of the Vermes.

Sympathetic nervous system.

Between stages K and L there may be seen short branches from the spinal nerves, which take a course towards the median line of the body, and terminate in small irregular cellular masses immediately dorsal to the cardinal veins (Pl. XVII. fig. 1, *sy. g.*). These form the first traces that have come under my notice of the sympathetic nervous system. In the youngest of my embryos in which I have detected these it has not been possible for me either definitely to determine the antero-posterior limits of the system, or to make certain whether the terminal masses of cells which form the ganglia are connected by a longitudinal commissure. In a stage slightly younger than L the ganglia are much more definite, the anterior one is situated in the cardiac region close to the end of the intestinal branch of the vagus, and the last of them quite at the posterior end of the abdominal cavity. The anterior ganglia are the largest; the commissural cord, if developed, is still very indistinct. In stage L the commissural cord becomes definite, though not very easy to see even in longitudinal sections, and the ganglia become so considerable as not to be easily overlooked. They are represented in Pl. XII. fig. 1, *sy. g.* and in Pl. XVII. fig. 2 in the normal position immediately above the cardinal veins. The branches connecting them with the trunks of the spinal nerves may still be seen without difficulty. In later stages these branches cannot so easily be made out in sections, but the ganglia themselves continue as fairly conspicuous objects. The segmental arrangement of the ganglia is shewn in Pl. XVII. fig. 3, a longitudinal and vertical section of an embryo between stages L and M with the junctions of the sympathetic ganglia and spinal nerves. The ganglia occupy the intervals between the successive segments of the kidneys.

The sympathetic system only came under my notice at a comparatively late period in my investigations, and the above facts do not in all points clear up its development[1]. My observations seem to point to the sympathetic system arising as an off-shoot from the cerebrospinal system. Intestinal branches would seem to be developed on the main nerve stems of this in the thoracic and abdominal regions, each of these then developes a ganglion, and the ganglia become connected by a longitudinal commissure. On this view a typical spinal nerve has the following parts: two roots, a dorsal and ventral, the dorsal one ganglionated, and three main branches, (1) a ramus dorsalis, (2) a ramus ventralis, and (3) a ramus intestinalis. This scheme may be advantageously compared with that of a typical cranial nerve according to Gegenbaur. It may be noted that it brings the sympathetic nervous system into accord with the other parts of the nervous system as a product of the epiblast, and derived from outgrowths from the neural axis. It is clear, however, that my investigations, though they may naturally be interpreted in this way, do not definitely exclude a completely different method of development for the sympathetic system.

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[1] The formation out of the sympathetic ganglia of the so-called paired suprarenal bodies is dealt with in connection with the vascular system. The original views of Leydig on these bodies are fully borne out by the facts of their development.

CHAPTER IX.

The Development of the Organs in the Head.

The Development of the Brain.

General History. In stage G the brain presents a very simple constitution (Pl. VI. fig. G), and is in fact little more than a dilated termination to the cerebro-spinal axis. Its length is nearly one-third that of the whole body, being proportionately very much greater than in the adult.

It is divided by very slight constrictions into three lobes, the posterior of which is considerably the largest. These are known as the fore-brain, the mid-brain, and the hind-brain. The anterior part of the brain is bent slightly downwards about an axis passing through the mid-brain. The walls of the brain, composed of several rows of elongated columnar cells, have a fairly uniform thickness, and even the roof of the hind-brain is as thick as any other part. Towards the end of stage G the section of the hind-brain becomes somewhat triangular with the apex of the triangle directed downwards.

In Pristiurus during stage H no very important changes take place in the constitution of the brain. In Scyllium, however, indications appear in the hind-brain of its future division into a cerebellum and medulla oblongata. The cavity of the anterior part dilates and becomes rounded, while that of the posterior part assumes in section an hour-glass shape, owing to an increase in the thickness of the lateral parts of the walls. At the same time the place of the original thick roof is taken by a very thin layer, which is formed not so much through a change in the character and arrangements of the cells composing the roof, as by a divarication of the two sides of the hind-brain, and the simultaneous introduction of a fresh structure in the form of a thin sheet of cells connecting dorsally the diverging lateral halves of this part of the brain. By stage I, the hind-brain in Pristiurus also acquires an hour-glass shaped section, but the roof has hardly begun to thin out (Pl. XIV. fig. 4*a* and 4*b*).

During stages I and K the cranial flexure becomes more and more pronounced, and causes the mid-brain definitely to form the termination of the long axis of the embryo (Pl. XIV. fig. 1, 2, etc.), and before the close of stage K a thin coating of white matter has appeared on the exterior of the whole brain, but no other histological changes of interest have occurred.

During stage L an apparent rectification of the cranial flexure commences, and is completed by stage Q. The changes involved in this process may be advantageously studied by comparing the longitudinal sections of the brain during stages L, P, and Q, represented in Pl. XV. fig. 1*a*, 5 and 7*a*.

It will be seen, first of all, that so far from the flexure of the brain itself being diminished, it is increased, and in P (fig. 5) the angle in the floor of the mid-brain becomes very acute indeed; in other words, the anterior part of the brain has been bent upon the posterior through nearly two right angles, and the infundibulum, or primitive front end of the brain, now points nearly directly backwards. At the same time the cerebral hemispheres have grown directly forwards, and if figures 1*a* and 5 in Plate XV. be compared it will be seen that in the older brain of the two the cerebral hemispheres have assumed a position which might be looked on as the result of their having been pushed dorsalwards and forwards against the mid-brain, and having in the process pressed in and nearly obliterated the original thalamencephalon. The thalamencephalon in fig. 1*a*, belonging to stage L, is relatively large, but in fig. 5, belonging to stage P, it only occupies a very small space between the front wall of the mid-brain and the hind wall of the cerebral hemispheres. It is therefore in part by the change in position of the cerebral hemispheres that the angle between the trabeculæ and parachordals becomes increased, *i.e.* their flexure *diminished*, while at the same time the flexure of the brain itself is *increased*. More important perhaps in the apparent rectification of the cranial flexure than any of the previously mentioned points, is the appearance of a bend in the hind-brain which tends to correct the original cranial flexure. The gradual growth of this fresh flexure can be studied in the longitudinal sections which have been represented. It is at its maximum in stage Q. This short preliminary sketch of the development of the brain as a whole will serve as an introduction to the history of the individual divisions of the brain.

Fore-brain. In its earliest condition the fore-brain forms a single vesicle without a trace of separate divisions, but buds off very early the optic vesicles, whose history is described with that of the eye (Pl. XIV. fig. 3, *op. v*). Between stages I and K the posterior part of the fore-brain sends outwards a papilliform process towards the exterior, which forms the rudiment of the pineal gland (Pl. XIV. fig. 1, *pn*). Immediately in front of the rudiment a constriction appears, causing a division of the fore-brain into a large anterior and a small posterior portion. This constriction is shallow at first, but towards the close of stage K becomes much deeper (Pl. XIV. fig. 2 and fig. 16*a*), leaving however the two cavities of the two divisions of the fore-brain united ventrally by a somewhat wide canal.

The posterior of the two divisions of the fore-brain forms the thalamencephalon. Its anterior wall adjoining the cerebral rudiment becomes excessively thin (Pl. XIV. fig. 11); and its base till the close of stage K is in close contact with the mouth involution, and presents but a very inconspicuous prominence which marks the eventual position of the infundibulum (Pl. XIV. fig. 9*a*, 12, 16, *in*). The anterior and larger division of the fore-brain forms the rudiment of the cerebral hemispheres and olfactory lobes. Up to stage K this rudiment remains perfectly simple, and exhibits no signs, either externally or internally, of a longitudinal constriction into two lobes. From the canal uniting the two divisions of the fore-brain (which eventually forms part of the thalamencephalon) there spring the hollow optic nerves. A slight ventral constriction separating the cerebral rudiment from that part of the brain where these are attached appears even before the close of stage K (Pl. XIV. fig. 11, *op.n*).

During stage L the infundibulum becomes much produced, and forms a wide sack in contact with the pituitary body, and its cavity communicates with that of the third ventricle by an elongated slit-like aperture. This may be seen by comparing Pl. XV. fig. 1*a* and 1*c*. In fig. 1*c* taken along the middle line, there is present a long opening into the infundibulum (*in*), which is shewn to be very narrow by being no longer present in fig. 1*a* representing a section slightly to one side of the middle line. During the same stage the pineal gland grows into a sack-like body, springing from the roof of the thalamencephalon, fig. 1*b*, *pn*. This latter (the thalamencephalon) is now dorsally separated from the cerebral rudiment by a deep constriction, and also ventrally by a less well marked constriction. At its side also a deep constriction is being formed in it, immediately behind the pineal gland. The cerebral rudiment is still quite unpaired and exhibits no sign of becoming constricted into two lobes.

During the next two stages the changes in the fore-brain are of no great importance, and I pass at once to stage O. The infundibulum is now nearly in the same condition as during stage L, though (as is well shewn in the figure of a longitudinal section of the next stage) it points more directly backwards than before. The remaining parts of the thalamencephalon have however undergone considerable changes. The more important of these are illustrated by a section of stage O, Pl. XV. fig. 3, transverse to the long axis of the embryo, and therefore, owing to the cranial flexure, cutting the thalamencephalon longitudinally and horizontally; and for stage P in a longitudinal and vertical section through the brain (Pl. XV. fig. 5). In the first place the roof of the thalamencephalon has become very much shortened by the approximation of the cerebral rudiment to the mid-brain. The pineal sack has also become greatly elongated, and its somewhat dilated extremity is situated between the cerebral rudiment and the external skin. It opens into the hind end of the third ventricle, and its posterior wall is continuous with the front wall of the mid-brain. The sides of the thalamencephalon have become much thickened, and form distinct optic thalami (*op.*) united by a very well marked posterior commissure (*p c.*). The anterior wall of the thalamencephalon as well as its roof are very thin. The optic nerves have become by stage O quite solid except at their roots, into which the ventricles of the fore-brain are for a short distance prolonged. This solidification is arrived at, so far as I have determined, without the intervention of a fold. The nerves are fibrous, and a commencement of the chiasma is certainly present. From the chiasma there appears to pass out on each side a band of fibres, which runs near the outer surface of the brain to the base of the optic lobes (mid-brain), and here the fibres of the two sides again cross.

By stage O important changes are perceptible in the cerebral rudiment. In the first place there has appeared a slight fold at its anterior extremity (Pl. XV. fig. 3, *x*), destined to form a vertical septum dividing it into two hemispheres, and secondly, lateral outgrowths (vide Pl. XV. fig. 2, *ol.l*), to form the olfactory lobes. Its thin posterior wall presents on each side a fold which projects into the central cavity. From the peripheral end of each olfactory lobe a nerve similar in its histological constitution to any other cranial nerve makes its appearance (Pl. XV. fig. 2); this divides into a number of branches, one of which passes into the connective tissue between the two layers of epithelium in each Schneiderian fold. On the root of this nerve there is a large development of ganglionic cells. I have not definitely observed its origin, but have no reason to doubt that it is a direct outgrowth from the olfactory lobe, exactly similar *in its mode of development* to any other nerve of the body.

The cerebral rudiment undergoes great changes during stage P. In addition to a great increase in the thickness of its walls, the fold which appeared in the last stage has grown backwards, and now divides it in front into two lobes, the rudiments of the cerebral hemispheres. The greater and posterior section is still however quite undivided, and the cavities of the lobes (lateral ventricles) though separated in front are still quite continuous behind. At the same time, the olfactory lobes, each containing a prolongation of the ventricle, have become much more pronounced (vide Pl. XV. fig. 4*a* and 4*c*, *ol.l*). The root of the olfactory nerve is now very thick, and the ganglion cells it contains are directly prolonged into the ganglionic portion of the olfactory bulb; in consequence of which it becomes rather difficult to fix on the exact line of demarcation between the bulb and the nerve.

Stage Q is the latest period in which I have investigated the development of the brain. Its structure is represented for this stage in general view in Pl. XV. fig. 6*a*, 6*b*, 6*c*, in longitudinal section in Pl. XV. fig. 7*a*, 7*b*, and in transverse section Pl. XV. fig. 8*a*—*d*. The transverse sections are taken from a somewhat older embryo than the longitudinal. In the thalamencephalon there is no fresh point of great importance to be noticed. The pineal gland remains as before, and has become, if anything, longer than it was, and extends further forwards over the summit of the cerebrum. It is situated, as might be expected, in the connective tissue within the cranial cavity (fig. 8*a*, *pn*), and does not extend outside the skull, as it appears to do, according to Götte's investigations, in Amphibians. Götte[1] compares the pineal gland with the long persisting pore which leads into the cavity of the brain in the embryo of Amphioxus, and we might add the Ascidians, and calls it "ein Umbildungsprodukt einer letzten Verbindung des Hirns mit der Oberhaut." This suggestion appears to me a very good one, though no facts have come under my notice which confirm it. The sacci vasculosi are perhaps indicated at this stage in the two lateral divisions of the trilobed ventricle of the infundibulum (fig. 8*c*).

The lateral ventricles (fig. 8*a*) are now quite separated by a median partition, and a slight external constriction marks the lobes of the two hemispheres; these, however, are still united by nervous structures for the greater part of their extent. The olfactory lobes are formed of a distinct bulb and stalk (fig. 8*a*, *ol.l*), and contain, as before, prolongations of the lateral ventricles. The so-called optic chiasma is very distinct (fig. 8*b*, *op.n*), but the fibres from the optic nerves appear to me simply to cross and not to intermingle.

The mid-brain. The mid-brain is at first fairly marked off from both the fore and hind brains, but less conspicuously from the latter than from the former. Its roof becomes progressively thinner and its sides thicker up to stage P, its cavity remaining quite simple. The thinness of the roof gives it, in isolated brains of stage P, a bilobed appearance, (vide Pl. XV. fig. 4*b*, *mb*, in which the distinctness of this character is by no means exaggerated). During stage Q it becomes really bilobed through the formation in its roof of a shallow median furrow,

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[1] *Ent. d. Unke*, p. 304.

(Pl. XV. fig. 8*b*). Its cavity exhibits at the same time the indication of a division into a central and two lateral parts.

The hind-brain. The hind-brain has at first a fairly uniform structure, but by the close of stage I, the anterior part becomes distinguished from the remainder by the fact, that its roof does not become thin as does that of the posterior part. This anterior, and *at first very insignificant portion*, forms the rudiment of the cerebellum. Its cavity is quite simple and is continued uninterruptedly into that of the remainder of the hind-brain. The cerebellum assumes in the course of development a greater and greater prominence, and eventually at the close of stage Q overlaps both the optic lobes in front and the medulla behind (Pl. XV. fig. 7*a*). It exhibits in surface-views of the hardened brain of stages P and Q the appearance of a median constriction, and the portion of the ventricle contained in it is prolonged into two lateral outgrowths (Pl. XV. fig. 8*c* and 8*d*, *cb*).

The posterior section of the hind-brain which forms the medulla undergoes changes of a somewhat complicated character. In the first place its roof becomes in front very much extended and thinned out. At the raphe, where the two lateral halves of the brain originally united, a separation, as it were, takes place, and the two sides of the brain become pushed apart, remaining united by only a very thin layer of nervous matter (Pl. XIV. fig. 6, iv. v.). As a result of this peculiar growth in the brain, the roots of the nerves of the two sides which were originally in contact at the dorsal summit of the brain become carried away from one another, and appear to arise at the sides of the brain (Pl. XIV. fig. 6 and 7). Other changes also take place in the walls of the brain. Each lateral wall presents two projections towards the interior (Pl. XIV. fig. 5*a*). The ventral of these vanish, and the dorsal approximate so as nearly to divide the cavity of the hind-brain, or fourth ventricle, into a large dorsal and a small ventral channel (Pl. XIV. fig. 6), and this latter becomes completely obliterated in the later stages. The dorsal pair, while approximating, also become more prominent, and stretch into the dorsal moiety of the fourth ventricle (Pl. XIV. fig. 6). They are still very prominent at stage Q (Pl. fig. XV. 8*d*, *f t*), and correspond in position with the fasciculi teretes of human anatomy. Part of the root of the seventh nerve originates from them. They project freely in front into the cavity of the fourth ventricle (Pl. XV. fig. 7 *f t*).

By stage Q restiform tracts are indistinctly marked off from the remainder of the brain, and are anteriorly continued into the cerebellum, of which they form the peduncles. Near their junction with the cerebellum they form prominent bodies (Pl. XV. fig. 7*a*, *r t*), which are regarded by Miklucho-Maclay[1] as representing the true cerebellum.

By stage O the medulla presents posteriorly, projecting into its cavity, a series of lobes which correspond with the main roots (not the branches) of the vagus and glosso-pharyngeal nerves (Pl. XVI. fig. 5). There appear to me to be present seven or eight projections: their number cannot however be quite certainly determined. The first of them belongs to the root of the glosso-pharyngeal, the next one is interposed between the glosso-pharyngeal and the first root of the vagus, and is without any corresponding nerve-root. The next five correspond to the five main roots of the vagus. For each projection to which a nerve pertains there is a special nucleus of nervous matter, from which the root springs. These nuclei do not stain like the remainder of the walls of the medulla, and stand out accordingly very conspicuously in stained sections.

The coating of white matter which appeared at the end of stage K, on the exterior of each lateral half of the hind-brain, extends from a point just dorsal to the attachment of the nerve-roots to the ventral edge of the medulla, and is specially connected with the tissue of the upper of the two already described projections into the fourth ventricle.

A rudiment of the tela vasculosa makes its appearance during stage Q, and is represented by the folds in the wall of the fourth ventricle in my figure of that stage (Pl. XV. fig. 7*a*, *t v*).

The development of the brain in Elasmobranchs has already been worked out by Professor Huxley, and a brief but in many respects very complete account of it is given in his recent paper on Ceratodus[2]. He says, pp. 30 and 31, "The development of the cerebral hemispheres in Plagiostome Fishes

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[1] *Das Gehirn d. Selachier*, Leipzig, 1870.

[2] *Proceedings of the Zoological Society*, 1876, Pt. I. p. 30 and 31.

differs from the process by which they arise in the higher Vertebrata. In a very early stage, when the first and second visceral clefts of the embryo Scyllium are provided with only a few short branchial filaments, the anterior cerebral vesicle is already distinctly divided into the thalamencephalon (from which the large infundibulum proceeds below, and the small tubular peduncle of the pineal gland above, while the optic nerve leaves its sides) and a large single oval vesicle of the hemispheres. On the ventral face of the integument covering these are two oval depressions, the rudimentary olfactory sacs.

"As development proceeds the vesicle of the hemispheres becomes divided by the ingrowth of a median longitudinal septum, and the olfactory lobes grow out from the posterior lateral regions of each ventricle thus formed, and eventually rise on to the dorsal faces of the hemispheres, instead of, as in most Vertebrata, remaining on their ventral sides. I may remark, that I cannot accept the views of Miklucho-Maclay, whose proposal to alter the nomenclature of the parts of the Elasmobranch's brain, appears to me to be based upon a misinterpretation of the facts of development."

The last sentence of the paragraph brings me to the one part on which it is necessary to say a few words, viz. the views of Miklucho-Maclay. His views have not received any general acceptance, but the facts narrated in the preceding pages shew, beyond a doubt, that he has 'misinterpreted' the facts of development, and that the ordinary view of the homology of the parts is the correct one. A comparison of the figures I have given of the embryo brain with similar figures of the brain of higher Vertebrates shews this point conclusively. Miklucho-Maclay has been misled by the large size of the cerebellum, but, as we have seen, this body does not begin to be conspicuous till late in embryonic life. Amongst the features of the embryonic brain of Elasmobranchs, the long persisting unpaired condition of the cerebral hemisphere, upon which so much stress has already been laid by Professor Huxley, appears to me to be one of great importance, and may not improbably be regarded as a real ancestral feature. Some observations have recently been published by Professor B. G. Wilder[1]

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[1] Anterior brain-mass with Sharks and Skates, *American Journal of Science and Arts*, Vol. XII. 1876.

upon this point, and upon the homologies and development of the olfactory lobes. Fairly good figures are given to illustrate the development of the cerebral hemispheres, but the conclusions arrived at are in part opposed to my own results. Professor Wilder says: "The true hemispheres are the lateral masses, more or less completely fused in the middle line, and sometimes developing at the plane of union a bundle of longitudinal commissural fibres. The hemispheres retain their typical condition as anterior protrusions of the anterior vesicle; but they lie mesiad of the olfactory lobes, *and in Mustelus at least seem to be formed after them*." The italics are my own. From what has been said above, it is clear that the statement italicised, for Scyllium at least, completely reverses the order of development. Still more divergent from my conclusions are Professor Wilder's statements on the olfactory lobes. He says: "The true olfactory lobe, or rhinencephalon, seems, therefore, to embrace only the hollow base of the crus, more or less thickened, and more or less distinguishable from the main mass as a hollow process. The olfactory bulb, with the more or less elongated crus of many Plagiostomes, seems to be developed independently, or in connection with the olfactory sack, as are the general nerves;" and again, "But the young and adult brains since examined shew that the ventricle (*i.e.* the ventricle of the olfactory lobe) ends as a rounded cul-de-sac before reaching the 'lobe'."

The majority of the statements contained in the above quotations are not borne out by my observations. Even the few preparations of which I have given figures, appear to me to prove that (1) the olfactory lobes (crura and bulbs) are direct outgrowths from the cerebral rudiment, and develope quite independently of the olfactory sack; (2) that the ventricle of the cerebral rudiment does not stop short at the base of the crus; (3) that from the bulb a nerve grows out which has a centrifugal growth like other nerves of the body, and places the central olfactory lobe in communication with the peripheral olfactory sack. In some other Vertebrates this nerve seems hardly to be developed, but it is easily intelligible, that if in the ordinary course of growth the olfactory sack became approximated to the olfactory lobe, the nerve which grew out from the latter to the sack might become so short as to escape detection.

Organs of Sense.

The olfactory organ. The olfactory pit is the latest formed of the three organs of special sense. It appears during a stage intermediate between *I* and *K*, as a pair of slight thickenings of the external epiblast, in the normal vertebrate position on the under side of the fore-brain immediately in front of the mouth (Pl. XIV. fig. 1 and 2, *ol*).

The epiblast cells which form this thickening are very columnar, but present no special peculiarities. Each thickened patch of skin soon becomes involuted as a shallow pit, which remains in this condition till the close of the stage *K*. The epithelium very early becomes raised into a series of folds (Schneiderian folds). These are bilaterally symmetrical, and diverge like the barbs of a feather from a median line (Pl. XIV. fig. 14). The nasal pits at the close of stage K are still separated by a considerable interval from the walls of the brain, and no rudiment of an olfactory lobe arises till a later period; but a description of the development of this as an integral part of the brain has already been given, p. 178.

Eye. The eye does not present in its early development any very special features of interest. The optic vesicles arise as hollow outgrowths from the base of the fore-brain (Pl. XIV. fig. 3, *op.v*), from which they soon become partially constricted, and form vesicles united to the base of the brain by comparatively narrow hollow stalks, the rudiments of the optic nerves. The constriction to which the stalk or optic nerve is due takes place from above and backwards, so that the optic nerves open into the base of the front part of the thalamencephalon (Pl. XIV. fig. 13*a*, *op n*). After the establishment of the optic nerves, there take place the formation of the lens and the pushing in of the anterior wall of the optic vesicle towards the posterior.

The lens arises in the usual vertebrate fashion. The epiblast in front of the optic vesicle becomes very much thickened, and then involuted as a shallow pit, which eventually deepens and narrows. The walls of the pit are soon constricted off as a nearly spherical mass of cells enclosing a very small central cavity, in some cases indeed so small as to be barely recognisable (Pl. XIV. fig. 7, *l*). The pushing in of the anterior wall of the optic vesicle towards the posterior takes place in quite the normal manner; but, as has been already noticed by Götte[1] and others, is not a simple mechanical result of the formation of the lens, as is shewn by the fact that the vesicle assumes a flattened form even before the appearance of the lens. The whole exterior of the optic cup becomes invested by mesoblast, but *no mesoblastic cells grow in between the lens and the adjoining wall of the optic cup.*

Round the exterior of the lens, and around the exterior and interior of the optic cup, there appear membrane-like structures, similar to those already described round the spinal cord and other organs. These membrane-like structures appear with a varying distinctness, but at the close of stage *K* stand out with such remarkable clearness as to leave no doubt that they are not artificial products (Pl. XIV. fig. 13*a*).[2] They form the rudiments of the hyaloid membrane and lens capsule. Similar, though less well marked membranes, may often be seen lining the central cavity of the lens and the space between the two walls of the optic cup. The optic cup is at first very shallow, but owing to the rapid growth of the free edge of its walls soon becomes fairly deep. The growth extends to the whole circumference of the walls except the point of entrance of the optic nerve (Pl. XIV. fig. 13*a*), where no growth takes place; here accordingly a gap is left in the walls, which forms the well known choroid slit. While this double walled cup is increasing in size, the wall lining the cavity of the cup becomes thick, and the outer wall very thin (fig. 13*a*). No further differentiations arise before the close of stage K.

The lens is carried outwards with the growth of the optic cup, leaving the cavity of the cup quite empty. It also grows in size, and its central cavity becomes larger. Still later its anterior wall becomes very thin, and its posterior wall thick, and doubly convex (fig. 13*a*). Its changes, however, so exactly correspond to those already known in other Vertebrates, that a detailed description of them would be superfluous.

No mesoblast passes into the optic cup round its edge, but a process of mesoblast, accompanied by a blood-vessel, passes into

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[1] *Entwickelungsgeschichte d. Unke.*

[2] The engraver has not been very successful in rendering these membranes.

the space between the lens and the wall of the optic cup through the choroid slit (fig. 13*a*, *ch*). This process of tissue is very easily seen, and swells out on entering the optic cup into a mushroom-like expansion. It forms the processus falciformis, and from it is derived the vitreous humour.

About the development of the parts of the eye, subsequently to stage *K*, I shall not say much. The iris appears during stage *O*, as an ingrowing fold of both layers of the optic cup with a layer of mesoblast on its outer surface, which tends to close over the front of the lens. Both the epiblast layers comprising the iris are somewhat atrophied, and the outer one is strongly pigmented. At stage O the mesoblast first also grows in between the external skin and the lens to form the rudiment of the mesoblastic structures of the eye in front of the lens. The layer, when first formed, is of a great tenuity.

The points in my observations, to which I attach the greatest importance, are the formation of the lens capsule and the hyaloid membrane; with the development of these may be treated also that of the vitreous humour and rudimentary *processus falciformis.* The development of these parts in Elasmobranchs has recently been dealt with by Dr Bergmeister[1], and his observations with reference to the vitreous humour and processus falciformis, the discovery of which in embryo Elasmobranchs is due to him, are very complete. I cannot, however, accept his view that the hyaloid membrane is a mesoblastic product. Through the choroid slit there grows, as has been said, a process of mesoblast, the processus falciformis, which on entering the optic cup dilates, and therefore appears mushroom-shaped in section. At the earliest stage (K) a blood-vessel appeared in connection with it, but no vascular structure came under my notice in the later stages. The structure of this process during stage P is shewn in Pl. XVI. fig. 6, *p. fal.*; it is there seen to be composed of mesoblast-cells with fibrous prolongations. The cells, as has been noticed by Bergmeister, form a special border round its dilated extremity. This process is formed much earlier than the vitreous humour, which is first seen in stage O. In hardened specimens this latter appears either as a gelatinous mass with a meshwork of fibres

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[1] *Embryologie d. Coloboms, Sitz. d. k. Akad. Wien,* Bd. LXXI. 1875.

or (as shewn in Pl. XVI. fig. 6) with elongated fibres proceeding from the end of the processus falciformis. These fibres are probably a product of the hardening reagent, but perhaps represent some preformed structure in the vitreous humour. I have failed to detect in it any cellular elements. It is more or less firmly attached to the hyaloid membrane.

On each side of the processus falciformis in stage P a slight fold of the optic cup is to be seen, but folds so large as those represented by Bergmeister have never come under my notice, though this may be due to my not having cut sections of such late embryos as he has. The hyaloid membrane appears long before the vitreous humour as a delicate basement membrane round the inner surface of the optic cup (Pl. XIV. fig. 13*a*), which is perfectly continuous with a similar membrane round the outer surface. In the course of development the hyaloid membrane becomes thicker than the membrane outside the optic cup, with which however it remains continuous. This is very clear in my sections of stage M. By stage O the membrane outside the cup has ceased to be distinguishable, but the hyaloid membrane may nevertheless be traced to the very edge of the cup round the developing iris; but does not unite with the lens capsule. It can also be traced quite to the junction of the two layers of the optic cup at the side of the choroid slit (Pl. XVI. fig. 6, *hy. m*). When the vitreous humour becomes artificially separated from the retina, the hyaloid membrane sometimes remains attached to the former, but at other times retains in preference its attachment to the retina. My observations do not throw any light upon the junction of the hyaloid membrane and lens capsule to form the suspensory ligament, nor have I ever seen (as described by Bergmeister) the hyaloid membrane extending across the free end of the processus falciformis and separating the latter from the vitreous humour. This however probably appears at a period subsequent to the latest one investigated by me. The lens capsule arises at about the same period as the hyaloid membrane, and is a product of the cells of the lens. It can be very distinctly seen in all the stages subsequent to its first formation. The proof of its being a product of the epiblastic lens, and not of the mesoblast, lies mainly in the fact of there being no mesoblast at hand to give rise to it at the time of its formation, vide Pl. XIV, fig. 13*a*. If the above observations are correct, it is clear that the hyaloid membrane and lens capsule are respectively products of the retina and lens; so that it becomes necessary to go back to the older views of Kölliker and others in preference to the more modern ones of Lieberkühn and Arnold. It would take me too far from my subject to discuss the arguments used by the later investigators to maintain their view that the hyaloid membrane and lens capsule are mesoblastic products; but it will suffice to say that the continuity of the hyaloid membrane over the pecten in birds is no conclusive argument against its retinal origin, considering the great amount of apparently independent growth which membranes, when once formed, are capable of exhibiting.

Bergmeister's and my own observations on the vitreous humour clearly prove that this is derived from an ingrowth through the choroid-slit. On the other hand, the researches of Lieberkühn and Arnold on the Mammalian Eye appear to demonstrate that a layer of mesoblast becomes in Mammalia involuted with the lens, and from this the vitreous humour (including the *membrana capsulo-pupillaris*) is said to be in part formed. Lieberkühn states that in Birds the vitreous humour is formed in a similar fashion. I cannot, however, accept his results on this point. It appears, therefore, that, so far as is known, all groups of Vertebrata, with the exception of Mammalia, conform to the Elasmobranch type. The differences between the types of Mammalia and remaining Vertebrata are, however, not so great as might at first sight appear. They are merely dependent on slight differences in the manner in which the mesoblast enters the optic cup. In the one case it grows in round one specialized part of the edge of the cup, *i.e.* the choroid-slit; in the other, round the whole edge, including the choroid-slit. Perhaps the mode of formation of the vitreous humour in Mammalia may be correlated with the early closing of the choroid-slit.

Auditory Organ. With reference to the development of the organ of hearing I have very little to say. Opposite the interval between the seventh and the glosso-pharyngeal nerves the external epiblast becomes thickened, and eventually involuted as a vesicle which remains however in communication with the exterior by a narrow duct. Towards the close of stage K the auditory sack presents three protuberances—one pointing forwards, a second backwards, and a third outwards. These are respectively the rudiments of the anterior and posterior vertical and external horizontal semicircular canals. These rudiments are easily visible from the exterior (Pl. XIV. fig. 2).

As has been already pointed out, the epiblast of Elasmobranchs during the early periods of development exhibits no division into an epidermic and a nervous layer, and in accordance with its primitive undifferentiated condition, those portions of the organs of sense which are at this time directly derived from the external integument are formed indiscriminately from the whole, and not from an inner or so-called nervous part of it only. In the Amphibians the auditory sack and lens are derived from the nervous division of the epiblast only, while the same division of the layer plays the major part in forming the olfactory organ. It is also stated that in Birds and Mammals the part of the epiblast corresponding to the nervous layer is alone concerned in the formation of the lens, though this does not appear to be the case with the olfactory or auditory organs in these groups of Vertebrates.

Mouth involution and Pituitary body.

The development of the mouth involution and the pituitary body is closely related to that of the brain, and may conveniently be dealt with here. The epiblast in the angle formed by the cranial flexure becomes involuted as a hollow process situated in close proximity to the base of the brain. This hollow process is the mouth involution, and it is bordered on its posterior surface by the front wall of the alimentary tract, and on its anterior by the base of the fore-brain.

The uppermost end of this does not till near the close of stage K become markedly constricted off from the remainder, but is nevertheless the rudiment of the pituitary body. Pl. XIV. figs. 9 *a* and 12 *m* shew in a most conclusive manner the correctness of the above account, and demonstrate that it is from the mouth involution, and not, as has usually been stated, from the alimentary canal, that the pituitary body is derived.

This fact was mentioned in my preliminary account of Elasmobranch development[1]; and has also been shewn to be the case in Amphibians by Götte[2], and in Birds by Mihalkowics[3]. The fact is of considerable importance with reference to speculations as to the meaning of this body.

Plate XIV. fig. 7 represents a transverse section through the head during a stage between I and K; but, owing to the cranial flexure, it cuts the fore part of the head longitudinally and horizontally, and passes through both the fore-brain (*fb*) and the hind-brain (*iv. v.*). Close to the base of the fore-brain are seen the mouth (*m*), and the pituitary involution from this (*pt*). In contact with the pituitary involution is the blind anterior termination of the throat, which a little way back opens to the exterior by the first visceral cleft (I. *v.c.*). This figure alone suffices to demonstrate the correctness of the above account of the pituitary body; but the truth of this is still further confirmed by other figures on the same plate (fig. 9 *a* and 12 *m*); in which the mouth involution is in contact with, but still separated from, the front end of the alimentary tract. By the close of stage K, the septum between the mouth and throat becomes pierced, and the two are placed in communication. This condition is shewn in Pl. XIV. fig. 16 *a*, and Pl. XV. fig. 1 *a*, 1 *c*, *pt*. In these figures the pituitary involution has become very partially constricted off from the mouth involution, though still in direct communication with it. In later stages the pituitary involution becomes longer and dilated terminally, while the passage connecting it with the mouth becomes narrower and narrower, and is finally reduced to a solid cord, which in its turn disappears. The remaining vesicle then becomes divided into lobes, and connects itself closely with the infundibulum (Pl. XV. figs. 5 and 6 *pt*). The later stages for Elasmobranchs are fully described by W. Müller in his im-

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[1] *Quarterly Journal of Microscopic Science*, Oct. 1874.

[2] *Entwicklungsgeschichte der Unke.* Götte was the first to draw attention to this fact. His observations were then shewn to hold true for Elasmobranchs by myself, and subsequently for Birds by Mihalkowics.

[3] *Arch. f. micr. Anat.* Vol. XI.

portant memoir on the Comparative Anatomy and development of this organ[1].

Development of the Cranial Nerves.

The present section deals with the whole development (so far as I have succeeded in elucidating it) of the cranial nerves (excluding the optic and olfactory nerves and the nerves of the eye-muscles) from their first appearance to their attainment of the adult condition. My description commences with the first development of the nerves, to this succeeds a short description of the nerves in the adult Scyllium, and the section is completed by an account of the gradual steps by which the adult condition is attained.

Early Development of the Cranial Nerves.—Before the close of stage H the more important of the cranial nerves make their appearance. The fifth and the seventh are the first to be formed. The fifth arises by stage G (Pl. XIV. fig. 3 V), near the anterior end of the hind-brain, as *an outgrowth from the extreme dorsal summit of the brain, in identically the same way as the dorsal root of a spinal nerve.*

The roots of the two sides sprout out from the summit of the brain, in contact with each other, and grow ventralwards, one on each side of the brain, in close contact with its walls. I have failed to detect more than one root for the two embryonic branches of the fifth (ophthalmic and mandibular), *and no trace of anterior or ventral root has been met with in any of my sections.*

The seventh nerve is formed nearly simultaneously with or shortly after the fifth, and some little distance behind and independently of it, opposite the anterior end of the thickening of the epiblast to form the auditory involution. It arises precisely like the fifth, from the extreme dorsal summit of the neural axis (Pl. XIV. fig. 4*a*, VII). So far as I have been able to determine, the auditory nerve and the seventh proper possess only a single root common to the two. There is no anterior root for the seventh any more than for the fifth.

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[1] W. Müller, Ueber Entwicklung und Bau d. Hypophysis u. d. Processus infundibuli cerebri, *Jenaische Zeitschrift*, Bd. VI.

Behind the auditory involution, at a stage subsequent to that in which the fifth and seventh nerves appear, there arise a series of roots from the dorsal summit of the hind-brain, which form the rudiments of the glosso-pharyngeal and vagus nerves. These roots are formed towards the close of stage H, but are still quite short at the beginning of stage I. Their manner of development resembles that of the previously described cranial nerves. The central ends of the roots of the opposite sides are at first in contact with each other, and there is nothing to distinguish the roots of the glosso-pharyngeal and of the vagus nerves from the dorsal roots of spinal nerves. Like the dorsal roots of the spinal nerves, they appear as a series of ventral prolongations of a continuous outgrowth from the brain, which outgrowth is moreover continuous with that for the spinal nerves[1]. The outgrowth of the vagus and glosso-pharyngeal nerves is not continuous with that of the seventh nerve. This is shewn by Pl. XIV. figs. 4*a* and 4*b*. The outgrowth of the seventh nerve though present in 4*a* is completely absent in 4*b* which represents a section just behind 4*a*.

Thus, by the end of stage I, there have appeared the rudiments of the 5th, 7th, 8th, 9th and 10th cranial nerves, all of which spring from the hind-brain. These nerves all develope precisely as do the posterior roots of the spinal nerves, and it is a remarkable fact *that hitherto I have failed to find a trace in the brain of a root of any cranial nerve arising from the ventral corner of the brain as do the anterior roots of the spinal nerves*[2].

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[1] In the presence of this continuous outgrowth of the brain from which spring the separate nerve stems of the vagus, may perhaps be found a reconciliation of the apparently conflicting statements of Götte and myself with reference to the vagus nerve. Götte regards the vagus as a single nerve, from its originating as an undivided rudiment; but it is clear from my researches that, for Elasmobranchs at least, this method of arguing will not hold good, since it would lead to the conclusion that all the spinal nerves were branches of one single nerve, since they too spring as processes from a continuous outgrowth from the brain!

[2] The conclusion here arrived at with reference to the anterior roots, is opposed to the observations of both Gegenbaur on Hexanchus, *Jenaische Zeitschrift*, Vol. VI, and of Jackson and Clarke on Echinorhinus, *Journal of Anatomy and Physiology*, Vol. X. These morphologists identify certain roots springing from the medulla below and behind the main roots of the vagus as true anterior roots of this nerve. The existence of these roots is not open to question, but without asserting that it is impossible for me to have failed to detect such roots had they been present in the embryo, I think I may maintain if these anterior roots are *not* present in the embryo, their identification as vagus roots must be abandoned; and they must be regarded as belonging to spinal nerves. This point is more fully spoken of at p. 205.

It is admittedly difficult to prove a negative, and it may still turn out that there are anterior roots of the brain similar to those of the spinal cord; in the mean time, however, the balance of evidence is in favour of there being none such. This at first sight appears a somewhat startling conclusion, but a little consideration shews that it is not seriously opposed to the facts which we know. In the first place it has been shewn by myself[1] that in Amphioxus (whose vertebrate nature I cannot doubt) only dorsal nerve-roots are present. Yet the nerves of Amphioxus are clearly mixed motor and sensory nerves, and it appears to me far more probable that Amphioxus represents a phase of development in which the nerves had not acquired two roots, rather than one in which the anterior root has been lost. In other words, the condition of the nerves in Amphioxus appears to me to point to the conclusion *that primitively the cranio-spinal nerves of vertebrates were nerves of mixed function with one root only, and that root a dorsal one; and that the present anterior or ventral root is a secondary acquisition.* This conclusion is further supported by the fact that the posterior roots develope in point of time before the anterior roots. If it be admitted that the vertebrate nerves primitively had only a single root, then the retention of that condition in the brain implies that this became differentiated from the remainder of the nervous system at a very early period before the acquirement of anterior nerve-roots, and that these eventually become developed only in the case of spinal nerves, and not in the case of the already highly modified cranial nerves.

Subsequent Changes of the Nerves.—To simplify my description of the subsequent growth of the cranial nerves, I have inserted a short description of their distribution in the adult. This is taken from a dissection of Scyllium Stellare, which like other species has some individualities of its own not found in the other Elasmobranchs. For points not touched on in this description I must refer the reader to the more detailed accounts of my predecessors, amongst whom may specially be mentioned Stannius[2] for Carcharias, Spinax, Raja, Chimæra,

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[1] *Journal of Anatomy and Physiology*, Vol. x.

[2] *Nervensystem d. Fische*, Rostock, 1849.

&c.; Gegenbaur[1] for Hexanchus; Jackson and Clarke[2] for Echinorhinus.

The ordinary nomenclature has been employed for the branches of the fifth and seventh nerves, though embryological data to be adduced in the sequel throw serious doubts upon it. Since I am without observations on the origin of the nerves to the muscles of the eyes, all account of these is omitted.

The fifth nerve arises from the brain by three roots[3]: (1) an anterior more or less ventral root; (2) a root slightly behind, but close to the former[4], formed by the coalescence of two distinct strands, one arising from a dorsal part of the medulla, and a second and larger from the ventral; (3) a dorsal and posterior root, in its origin quite distinct and well separated from the other two, and situated slightly behind the dorsal strand of the second root. This root a little way from its attachment becomes enclosed for a short distance in the same sheath as the dorsal part of the second root, and a slight mixture of fibres seems to occur, but the majority of its fibres have no connection with those of the second root. The first and second roots of the fifth appear to me partially to unite, but before their junction the ramus ophthalmicus profundus is given off from the first of them.

The fifth nerve, according to the usual nomenclature, has three main divisions. The first of these is the ophthalmic. It is formed by the coalescence of two entirely independent branches of the fifth, which unite on leaving the orbit. The dorsalmost of these, or ramus ophthalmicus superficialis, originates from the third and posterior of the roots of the fifth, nearly the whole of which appears to enter into its formation. This root is situated on the dorsal part of the "lobi trigemini," *at a point posterior to that of the other roots of the fifth or even of the seventh nerve.* The branch itself enters the orbit by a separate foramen, and, keeping on the dorsal side of it, reenters the cartilage at its anterior wall, and is there joined by the *ramus ophthalmicus profundus.* This latter nerve arises from the anterior root of the fifth, separately pierces the wall of the orbit, and takes a course slightly ventral to the superior ophthalmic nerve, but does not (as is usual with Elasmobranchs) run below the superior rectus and superior oblique muscles of the eye. The nerve formed by the coalescence of the superficial and deep ophthalmic branches courses a short way below the surface, and supplies the mucous canals of the front of the snout. It is a purely sensory nerve. Strong grounds will be adduced in the sequel for regarding the *ramus ophthalmicus superficialis,* though not the *ophthalmicus profundus,* as in reality a branch of the seventh, and not of the fifth nerve.

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[1] *Jenaische Zeitschrift*, Vol. VI.

[2] *Journal of Anatomy and Physiology*, Vol. X.

[3] My results with reference to these roots accord exactly, so far as they go, with the more carefully worked out conclusions of Stannius, *loc. cit.* p. 29 and 30.

[4] The root of the seventh nerve cannot properly be distinguished from this root.

The second division of the fifth nerve is the superior maxillary, which appears to me to arise from both the first and second roots of the fifth, though mainly from the first. It divides once into two main branches. The first of these—the buccal nerve of Stannius—after passing forwards along the base of the orbit takes its course obliquely across the palatine arch and behind and below the nasal sack, supplying by the way numerous mucous canals, and dividing at last into two branches, one of these passing directly forwards on the ventral surface of the snout, and the second keeping along the front border of the mouth. The second division of the superior maxillary nerve (superior maxillary of Stannius), after giving off a small branch, which passes backwards in company with a branch from the inferior maxillary nerve to the levator maxillæ superioris, itself keeps close to the buccal nerve, and eventually divides into numerous fine twigs to the mucous canals of the skin at the posterior region of the upper jaw. It anastomoses with the buccal nerve. The inferior maxillary nerve arises mainly from the second root of the fifth. After sending a small branch to the levator maxillæ superioris, it passes outwards along the line separating the musculus adductor mandibulæ from the musculus levator labii superioris, and after giving branches to these muscles takes a course forward along the border of the lower jaw. It appears to be a mixed motor and sensory nerve.

The seventh or facial nerve arises by a root close to, but behind and below the second root of the fifth, and is intimately fused with this. It divides almost at once into a small anterior branch and large posterior.

The anterior branch is the palatine nerve. It gives off at first one or two very small twigs, which pursue a course towards the spiracle, and probably represent the spiracular nerves of other Elasmobranchs. Immediately after giving off these branches it divides into two stems, a posterior smaller and an anterior larger one. The former eventually takes a course which tends towards the angle of the jaw, and is distributed to the mucous membrane of the roof of the mouth, while the larger one bends forwards and supplies the mucous membrane at the edge of the upper jaw. The main stem of the seventh, after giving off a branch to the dorsal section of the musculus constrictor superficialis, passes outwards to the junction of the upper and lower jaws, where it divides into two branches, an anterior superficial branch, which runs immediately below the skin on the surface of the lower jaw, and a second branch, which takes a deep course along the posterior border of the lower jaw, between it and the hyoid, and sends a series of branches backwards to the ventral section of the musculus constrictor superficialis. The main stem of the facial is mixed motor and sensory. I have not noticed a dorsal branch, similar to that described by Jackson and Clarke.

The auditory nerve arises immediately behind the seventh, but requires no special notice here. A short way behind the auditory is situated the root of the glossopharyngeal nerve. This nerve takes an oblique course backwards through the skull, and gives off in its passage a very small dorsal branch, which passes upwards and backwards through the cartilage towards the roof of the skull. At the point where the main stem leaves the cartilage it divides into two branches, an anterior smaller branch to the hinder border of the hyoid arch, and a posterior and larger one to anterior border of the first branchial arch. It forks, in fact, over the first visceral cleft.

The vagus arises by a great number of distinct strands from the sides of the medulla. In the example dissected there were twelve in all. The anterior three of these were the largest; the middle one having the most ventral origin. The next four were very small and in pairs, and were separated by a considerable interval from the next four, also very small, and these again by a marked interval from the hindermost strand.

The common stem formed by the junction of these gives off immediately on leaving the skull a branch which forks on the second branchial cleft: a second for the third cleft is next given off; the main stem then divides into a dorsal branch — the lateral nerve — and a ventral one—the branchio-intestinal nerve—which, after giving off the branches for the two last branchial clefts, supplies the heart and intestinal tract. The lateral nerve passes back towards the posterior end of the body, internal to the lateral line, and between the dorso-lateral and ventro-lateral muscles. It gives off at its origin a fine nerve, which has a course nearly parallel to its own. The main stem of the vagus, at a short distance from its central end, receives a nerve which springs from the ventral side of the medulla, on about a level with the most posterior of the true roots of the vagus. This small nerve corresponds with the ventral or anterior roots of the vagus described by Gegenbaur, Jackson, and Clarke (though in the species investigated by the latter authors these roots did not join the vagus, but the anterior spinal nerves). Similar roots are also mentioned by Stannius, who found two of them in the Elasmobranchs dissected by him; it is possible that a second may be present in Scyllium, but have been overlooked by me, or perhaps may have been exceptionally absent in the example dissected.

The Fifth Nerve. The thinning of the roof of the brain, in the manner already described, produces a great change in the apparent position of the roots of all the nerves. The central ends of the rudiments of the two sides are, as has been mentioned, at first in contact dorsally; but, when by the growth of the roof of the brain its two lateral halves become pushed apart, the nerves also shift their position and become widely separated. The roots of the fifth nerve are so influenced by these changes that they spring from the brain about half way up its sides, and a little ventral to the border of its thin roof. While this change has been taking place in the point of attachment of the fifth nerve, it has not remained in other respects in a stationary condition.

During stage H it already exhibits two distinct branches known as the mandibular and ophthalmic. These branches first lie outside a section of the body cavity which exists in the front part of the head. The ophthalmic branch of the fifth being situated near the anterior end of this, and the mandibular near the posterior end.

In stage I the body cavity in this part becomes divided into two parts one behind the other, the posterior being situated in the mandibular arch. The bifurcation of the nerve then takes place over the summit of the posterior of the two divisions of the body cavity, Pl. XIV. fig. 9 *b* V. and 10 V, &c., and at first both branches keep close to the sides of this.

The anterior or ophthalmic branch of the fifth soon leaves the walls of the cavity just spoken of and tends towards the eye, and there comes in close contact with the most anterior section of the body cavity which exists in the head. These relations it retains unchanged till the close of stage K. Between stages I and K it may easily be seen from the surface; but, before the close of stage K, the increased density of the tissues renders it invisible in the living embryo.

The posterior branch of the fifth extends downwards into the mandibular arch in close contact with the posterior and outer wall of the body space already alluded to. At first no branches from it can be seen, but I have detected by the close of stage K, by an examination of the living embryo, a branch springing from it a short way from its central extremity, and passing forwards, Pl. XIV. fig. 2 V. This branch I take to be the rudiment of the superior maxillary division of the fifth nerve. It is shewn in section, Pl. XIV. fig. 15 *a* V.

In the stages after K the anatomy of the nerves becomes increasingly difficult to follow, and accordingly I must plead indulgence for the imperfections in my observations on all the nerves subsequently to this date. In the fifth I find up to stage O a single ophthalmic branch (Pl. XVI. fig. 4*b* V *op. th.*), which passes forwards slightly dorsal to the eye and parallel and ventral to a branch of the seventh, which will be described when I come to that nerve. I have been *unable* to observe that this branch divides into a ramus superficialis and ramus profundus, and subsequently to stage O I have no observations on it.

By stage O the fifth may be observed to have two very distinct roots, and a large ganglionic mass is developed close to their junction (Gasserian ganglion), Pl. XVI. fig. 4 *a*. But in addition to this ganglionic enlargement, all of the branches have special ganglia of their own, Pl. XVI. fig. 4 *b*.

Summary. The fifth nerve has almost from the beginning two branches, the ophthalmic (probably the inferior ophthalmic of the adult) and the inferior maxillary. The superior maxillary nerve arises later than the other two as a branch from the inferior, originating comparatively far from its root. There is at first but a single root for the whole nerve, which subsequently becomes divided into two. Ganglionic swellings are developed on the common stem and main branches of the nerve.

A general view of the nerve is shewn in the diagram in Pl. XVI. fig. 1.

Seventh and Auditory Nerves.—There appears in my earliest sections a single large rudiment in the position of the seventh and auditory nerves; but in longitudinal sections of an embryo somewhat older than stage I, in which the auditory organ forms a fairly deep pit, still widely open to the exterior, there are to be seen immediately in front of the ear the rudiments of two nerves, which come into contact where they join the brain and have their roots still closely connected at the end of stage K (Pl. XIV. fig. 10 and 15 *a* and 15 *b*). The anterior of these pursues a straight course to the hyoid arch (Pl. XIV. fig. 10, VII.), the second of the two (Pl. XIV. fig. 10, *au. n.*), which is clearly the rudiment of the auditory nerve, developes a ganglionic enlargement and, turning backward, closely hugs the ventral wall of the auditory involution.

The observation just recorded appears to lead to the following conclusions with reference to the development of the auditory nerve. A single rudiment arises from the brain for the auditory and seventh nerves. This rudiment subsequently becomes split into two parts, an anterior to form the seventh nerve, and a posterior to form the auditory nerve. The ganglionic part of the auditory nerve is derived from the primitive outgrowths from the brain, and not from the auditory involution. I do not feel perfectly confident that an independent origin of the auditory nerve might not have escaped my notice; but, admitting the correctness of the view which attributes to the seventh and auditory a common origin, it follows that the auditory nerve primitively arose in connection with the seventh, of which it may either, as Gegenbaur believes, be a distinct part—the ramus dorsalis—or else may possibly have formed part of a commissure, homologous with that uniting the dorsal roots of the spinal nerves, connecting the seventh with the glossopharyngeal nerve. In either case it must be supposed secondarily to have become separate and independent in consequence of the development of the organ of hearing.

My sections of embryos of stage K and the subsequent stages do not bring to light many new facts with reference to the auditory nerve: they demonstrate however that its ganglionic part increases greatly in size, and in stage O there is a distinct root for the auditory nerve in contact with that for the seventh.

The history of the seventh nerve in its later stages presents points of great interest. Near the close of stage K there may be observed, in the living embryos and in sections, two branches of the seventh in addition to the original trunk to the hyoid arch, both arising from its anterior side; one passes straight forwards close to the external skin, but is at first only traceable a short way in front of the fifth, and a second passes downwards into the mandibular arch in such a fashion, that the seventh nerve forks over the hyomandibular cleft (vide Pl. XIV. fig. 2, VII.; 15 *a*, VII.). My sections shew both these branches with great clearness. A third branch has also come under my notice, whose course leads me to suppose that it supplies the roof of the palate.

In the later stages my attention has been specially directed to the very remarkable anterior branch of the seventh. This may, in stages L to O, be traced passing on a level with the root of the fifth nerve above the eye, and apparently terminating in branches to the skin in front of the eye (Pl. XVI. fig. 3, VII.; 4 *a*, VII. *a*). It courses close beneath the skin (though this does not appear in the sections represented on account of their obliqueness), and runs parallel and dorsal to the ophthalmic branch of the fifth nerve, and may easily be seen in this position in longitudinal sections belonging to stage O; but its changes after this stage have hitherto baffled me, and its final fate is therefore, to a certain extent, a matter of speculation.

The two other branches of the seventh, viz., the hyoid or main branch and mandibular branch, retain their primitive arrangement till the close of stage O.

The fate of the remarkable anterior branch of the seventh nerve is one of the most interesting points which has started up in the course of my investigations on the development of the cranial nerves, and it is a matter of very great regret to me that I have not been able to clear up for certain its later history.

Its primitive distribution leads to the supposition that it becomes the nerve known in the adult as the *ramus ophthalmicus superficialis of the fifth nerve*, and this is the view which I admit myself to be inclined to adopt. There are several points in the anatomy of this nerve in the adult which tell in favour of accepting this view with reference to it. In the first place, the ramus ophthalmicus superficialis rises from the brain (vide description above, p. 194), quite independently of the ramus ophthalmicus profundus, and not in very close connection with the other branches of the fifth, and also considerably behind these, quite as far back indeed as the ventral root of the seventh. There is therefore nothing in the position of its root opposed to its being regarded as a branch of the seventh nerve. Secondly, its distribution, which might at first sight be regarded as peculiar, presents no very strange features if it is looked on as a ramus dorsalis of the seventh, whose apparent anterior instead of dorsal course is due to the cranial flexure. If, however, the distribution of the ramus ophthalmicus superficialis is used as an argument against my view, a satisfactory reply is to be found in the fact that a branch of the seventh nerve certainly has the distribution in question *in the embryo*, and that there is no reason why it should not retain it *in the adult.*

Finally, the junction of the two rami ophthalmici, most remarkable if they are branches of a single nerve, would present nothing astonishing when they are regarded as branches of two separate nerves.

If this view be adopted, certain modifications of the more generally accepted views of the morphology of the cranial nerves will be necessitated; but this subject is treated of at the end of this section.

Some doubt hangs over the fate of the other branches of the seventh nerve, but their destination is not so obscure as that of the anterior branch. The branch to the roof of the mouth can be at once identified as the 'palatine nerve', and it only remains to speak of the mandibular branch.

It may be noticed first of all with reference to this branch, that the seventh behaves precisely like the less modified succeeding cranial nerves. It forks in fact over a visceral cleft (the hyomandibular) the two sides of which it supplies; the branch at the anterior side of the cleft is the later developed and smaller of the two. There cannot be much doubt that the mandibular branch must be identified with the spiracular nerve (præ-spiracular branch Jackson and Clarke) of the adult, and if the chorda tympani of Mammals is correctly regarded as the mandibular branch of the seventh nerve, then the spiracular nerve must represent it. Jackson and Clarke[1] take a different view of the homology of the chorda tympani, and regard it as equivalent to the ramus mandibularis internus (one of the two branches into which the seventh eventually divides), because this nerve takes its course over the ligament connecting the mandible with the hyoid. This view I cannot accept so long as it is admitted that the chorda tympani is the branch of a cranial nerve supplying the anterior side of a cleft. The ramus mandibularis internus, instead of forming with the main branch of the seventh a fork over the spiracle, passes to its destination completely behind and below the spiracle, and therefore fails to fulfil the conditions requisite for regarding it as a branch to the anterior wall of a visceral cleft. It is indeed clear that the ramus mandibularis internus cannot be identified with the embryonic mandibular branch of the seventh (which passes above the spiracle or hyomandibular cleft) when there is

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[1] *Loc. cit.*

present in the adult another nerve (the spiracular nerve), which exactly corresponds in distribution with the embryonic nerve in question. My view accords precisely with that already expressed by Gegenbaur in his masterly paper on the nerves of Hexanchus, in which he distinctly states that he looks upon the spiracular nerve as the homologue of an anterior branchial branch of a division of the vagus. In the adult the spiracular nerve is sometimes represented by one or two branches of the palatine, *e.g.* Scyllium, but at other times arises independently from the main stem of the seventh[1]. The only difficulty in my identification of the embryonic mandibular branch with the adult spiracular nerve, is the extremely small size of the latter in the adult, compared with the size of mandibular in the embryo; but it is hardly surprising to find an atrophy of the spiracular nerve accompanying an atrophy of the spiracle itself. The palatine appears to me to have been rightly regarded by Jackson and Clarke as the great superficial petrosal of Mammals.

On the common root of the branches of the seventh nerve, as well as on its hyoid branch, ganglionic enlargements are present at an early period of development.

The Glossopharyngeal and Vagus Nerves. Behind the ear there are formed a series of five nerves which pass down to respectively the first, second, third, fourth and fifth visceral arches.

For each arch there is thus one nerve, whose course lies close to the posterior margin of the preceding cleft, a second anterior branch being developed later. These nerves are connected with the brain (as I have determined by transverse sections) by roots at first attached to the dorsal summit, but eventually situated about half-way down the sides (Pl. XIV. fig. 6), nearly opposite the level of the process which divides the ventricle of the hind-brain into a dorsal and a ventral moiety. The foremost of these nerves is the glossopharyngeal. The next four are, as has been shewn by Gegenbaur[2], equivalent to four independent nerves, but form, together with the glossopharyngeal, a compound nerve, which we may briefly call the vagus.

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[1] Hexanchus, Gegenbaur, *Jenaische Zeitschrift*, Vol. VI.

[2] *Loc. cit.*

This compound nerve by stage K attains a very complicated structure, and presents several remarkable and unexpected features. Since it has not been possible for me completely to elucidate the origin of all its various parts, it will conduce to clearness if I give an account of its structure during stage K or L, and then return to what facts I can mention with reference to its development. Its structure during these stages is represented on the diagram, Pl. XVI. fig. 1. There are present five branches, viz. the glossopharyngeal and four branches of the vagus, arising probably by a considerably greater number of strands from the brain[1]. All the strands from the brain are united together by a thin commissure, *Vg. com.*, continuous with the commissure of the posterior roots of the spinal nerves, and from this commissure the five branches are continued obliquely ventralwards and backwards, and each of them dilates into a ganglionic swelling. They all become again united together by a second thick commissure, which is continued backwards as the intestinal branch of the vagus nerve *Vg. in.* The nerves, however, are continued ventralwards each to its respective arch. From the hinder part of the intestinal nerve springs the lateral nerve *n.l.*, at a point whose relations to the branches of the vagus I have not certainly determined.

The whole nerve-complex formed by the glossopharyngeal and the vagus nerves cannot of course be shewn in any single section. The various roots are shewn in Pl. XVI. fig. 5. The dorsal commissure is represented in longitudinal section in Pl. XIV. fig. 15 *b*, *com.*, and in transverse section in Pl. XVI. fig. 2 *Vg, com.* The lower commissure continued as the intestinal nerve is shewn in Pl. XIV. fig. 15 *a*, *Vg.*, and as seen in the living embryo in Pl. XIV. figs. 1 and 2. The ganglia are seen in Pl. XIV. fig. 6, *Vg.* The junction of the vagus and glossopharyngeal nerves is shewn in Pl. XIV. fig. 10. My observations have not taught me much with reference to the origin of the two commissures, viz. the dorsal one and the one which forms the intestinal branch of the vagus. Very possibly they originate as a single commissure which becomes longitudinally seg-

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[1] In the diagram there are only five strands represented. This is due to the fact that I have not certainly made out their true number.

mented. It deserves to be noticed that the dorsal commissure has a long stretch, from the last branch of the vagus to the first spinal nerve, during which it is not connected with the root of any nerve; vide fig. 15 *b*, *com.* This space probably contained originally the now lost branches of the vagus. In many transverse sections where the dorsal commissure might certainly be expected to be present it cannot be seen, but this is perhaps due to its easily falling out of the sections. I have not been able to prove that the commissure is continued forwards into the auditory nerve.

The relation of the branches of the vagus and glossopharyngeal to the branchial clefts requires no special remark. It is fundamentally the same in the embryo as in the adult. The branches at the posterior side of the clefts are the first to appear, those at the anterior side of the clefts being formed subsequently to stage K.

One of the most interesting points with reference to the vagus is the number of separate strands from the brain which unite to form it. The questions connected with these have been worked out in a masterly manner, both from an anatomical and a theoretical standpoint, by Professor Gegenbaur[1]. It has not been possible for me to determine the exact number of these in my embryos, nor have I been able to shew whether they are as numerous at the earliest appearance of the vagus as at a later embryonic period. The strands are connected (Pl. XVI. fig. 5) with separate ganglionic centres in the brain, though in several instances more than one strand is connected with a single centre. In an embryo between stage O and P more than a dozen strands are present. In an adult Scyllium I counted twelve separate strands, but their number has been shewn by Gegenbaur to be very variable. It is possible that they are remnants of the roots of the numerous primary branches of the vagus which have now vanished; and this perhaps is the explanation of their variability, since in the case of all organs which are on the way to disappear variability is a precursor of disappearance.

A second interesting point is the presence of the two connecting commissures spoken of above. It was not till com-

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[1] *Loc. cit.*

paratively late in my investigations that I detected the dorsal one. This has clearly the same characters as the dorsal commissure already described as connecting the roots of all the spinal nerves, and is indeed a direct prolongation of this. It becomes gradually thinner and thinner, and finally ceases to be observable by about the close of stage L. It is of importance as shewing the similarity of the branches of the vagus to the dorsal roots of the spinal nerves. The ventral of the two commissures persists in the adult as the common stem from which all the branches of the vagus successively originate, and is itself continued backwards as the intestinal branch of the vagus. The glossopharyngeal nerve alone becomes eventually separated from the succeeding branches. Stannius and Gegenbaur have, as was mentioned above, detected in adult Elasmobranchs roots which join the vagus, and which resemble the anterior or ventral roots of spinal nerves; and I have myself described one such root in the adult Scyllium. I have searched for these in my embryos, but without obtaining conclusive results. In the earliest stages I can find no trace of them, but I have detected in stage L one anterior root on debatable border-land, which may conceivably be the root in question, but which I should naturally have put down for the root of a spinal nerve. Are the roots in question to be regarded as proper roots of the vagus, or as ventral roots of spinal nerves whose dorsal roots have been lost? The latter view appears to me the most probable one, partly from the embryological evidence furnished by my researches, which is clearly opposed to the existence of anterior roots in the brain, and partly from the condition of these roots in Echinorhinus, in which they join the succeeding spinal nerves and not the vagus[1]. The similar relations of the apparently homologous branch or branches in many Osseous Fish may also be used as an argument for my view.

If, as seems probable, the roots in question become the hypoglossal nerve, this nerve must be regarded as formed from the anterior roots of one or more spinal nerves. Without embryological evidence it does not however seem possible to decide whether the hypoglossal nerve contains elements only of anterior roots or of both anterior and posterior roots.

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[1] Vide Jackson and Clarke *loc. cit.* The authors take a different view to that here advocated, and regard the ventral roots described by them as having originally belonged to the vagus.

Mesoblast of the Head.

Body Cavity and Myotomes of the Head.—During stage F the appearance of a cavity on each side in the mesoblast of the head was described. (Vide Pl. IX. fig. 3 *b* and 6 *pp.*) These cavities end in front opposite the blind anterior extremity of the alimentary canal; behind they are continuous with the general body-cavity. I propose calling them *the head-cavities.* The cavities of the two sides have no communication with each other.

Coincidently with the formation of an outgrowth from the throat to form the first visceral cleft, the head-cavity on each side becomes divided into a section in front of the cleft and a section behind the cleft (vide Pl. XIV. fig. 4 *a* and 4 *b pp.*); and during stage H it becomes, owing to the formation of a second cleft, divided into three sections: (1) a section in front of the first or hyomandibular cleft; (2) a section in the hyoid arch between the hyomandibular cleft and the hyobranchial or first branchial cleft; (3) a section behind the first branchial cleft.

The section in front of the hyomandibular cleft stands in a peculiar relation to the two branches of the fifth nerve. The ophthalmic branch of the fifth lies close to the outer side of its anterior part, the mandibular branch close to the outer side of its posterior part. During stage I this front section of the head-cavity grows forward, and becomes divided, without the intervention of a visceral cleft, into an anterior and posterior division. The anterior lies close to the eye, and in front of the commencing mouth involution, and is connected with the ophthalmic branch of the fifth nerve. The posterior part lies completely within the mandibular arch, and is closely connected with the mandibular division of the fifth nerve.

As the rudiments of the successive visceral clefts are formed, the posterior part of the head-cavity becomes divided into successive sections, there being one section for each arch. Thus the whole head-cavity becomes on each side divided into (1) a premandibular section; (2) a mandibular section; (3) a hyoid section; (4) sections in the branchial arches.

The first of these divisions forms a space of a considerable size, with epithelial walls of somewhat short columnar cells. It is situated close to the eye, and presents a rounded or sometimes triangular figure in sections (Pl. XIV. fig. 7, 9 *b* and 16 *b*, I. *pp.*). The ophthalmic branch of the fifth nerve passes close to its superior and outer wall.

Between stages I and K the anterior cavities of the two sides are prolonged ventralwards and meet below the base of the fore-brain (Pl. XIV. fig. 8, I. *pp.*). The connection between the two cavities appears to last for a considerable time, and still persists at the close of stage L. The anterior or premandibular pair of cavities are the only parts of the body-cavity within the head which unite ventrally. In the trunk, however, the primitively independent lateral halves of the body-cavity always unite in this way. The section of the head-cavity just described is so similar to the remaining posterior sections that it must be considered as equivalent to them.

The next division of the head-cavity, which from its position may be called the mandibular cavity, presents during the stages I and K a spatulate shape. It forms a flattened cavity, dilated dorsally, and produced ventrally into a long thin process parallel to the hyomandibular gill-cleft, Pl. XIV. fig. 1 *pp.* and fig. 7, 9 *b* and 15 *a*, 2 *pp.* Like the previous space it is lined by a short columnar epithelium.

The fifth nerve, as has already been mentioned, bifurcates over its dorsal summit, and the mandibular branch of that nerve passes down on its posterior and outer side. The mandibular aortic arch is situated close to its inner side, Pl. XIV. fig. 7. Towards the close of this period the upper part of the cavity atrophies. Its lower part also becomes much narrowed, but its walls of columnar cells persist and lie close to one another. The outer or somatic wall becomes very thin indeed, the splanchnic wall, on the other hand, thickens and forms a layer of several rows of elongated cells. This thicker wall is on its inner side separated from the surrounding tissue by a small space lined by a membrane-like structure. In each of the remaining arches there is a segment of the original body-cavity fundamentally similar to that in the mandibular arch. A dorsal dilated portion appears, however, to be present in the third or hyoid section alone, and even there disappears by the close of stage K. The cavities in the posterior parts of the head become much reduced like those in its anterior part, though at rather a later period. Their walls however persist, and become more columnar. In Pl. XIV. fig. 13 *b, pp.*, is represented the cavity in the last arch but one, at a period when the cavity in the mandibular arch has become greatly reduced. It occupies the same position on the outer side of the aortic trunk of its arch as does the cavity in the mandibular arch (Pl. XIV. fig. 7, 2*pp*). In Torpedo embryos the head-cavity is much smaller, and atrophies earlier than in the embryos of Pristiurus and Scyllium.

It has been shewn that, with the exception of the most anterior, the divisions of the body-cavity in the head become atrophied, *not so however their walls.* The cells forming these become elongated, and by stage N become distinctly developed into muscles. Their exact history I have not followed in its details, but they almost unquestionably become the musculus contrictor superficialis and musculus interbranchialis[1]; and probably also musculus levator mandibuli and other muscles of the front part of the head.

The most anterior cavity close to the eye remains unaltered much longer than the remaining cavities, and its two halves are still in communication at the close of stage L. I have not yet succeeded in tracing the subsequent fate of its walls, *but think it probable that they develope into the muscles of the eye.* The morphological importance of the sections of the body-cavity in the head cannot be over-estimated, and the fact that the walls become developed into the muscular system of the head renders it almost certain *that we must regard them as equivalent to the muscle-plates of the body, which originally contain, equally with those of the head, sections of the body-cavity.* If this determination is correct, there can be no doubt that they ought to serve as valuable guides to the number of segments which have coalesced to form the head. This point is, however, discussed in a subsequent section.

General mesoblast of the head.—In stage G no mesoblast is present in the head, except that which forms the walls of the head-cavity.

During stage H a few cells of undifferentiated connective

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[1] Vide Vetter, *Die Kiemen und Kiefermusculatur d. Fische. Jenaische Zeitschrift*, Vol. VII.

tissue appear around the stalk of the optic vesicle, and in the space between the front end of the alimentary tract and the base of the brain in the angle of the cranial flexure. They are probably budded off from the walls of the head-cavities. Their number rapidly increases, and they soon form an investment surrounding all the organs of the head, and arrange themselves as a layer, between the walls of the roof of the fore and mid-brain and the external skin. At the close of stage K they are still undifferentiated and embryonic, each consisting of a large nucleus surrounded by a very delicate layer of protoplasm produced into numerous thread-like processes. They form a regular meshwork, the spaces of which are filled up by an intercellular fluid.

I have not worked out the development of the cranial and visceral skeleton; but this has been made the subject of an investigation by Mr Parker, who is more competent to deal with it than any other living anatomist. His results were in part made known in his lectures before the Royal College of Surgeons[1], and will be published in full in the *Transactions of the Zoological Society*.

All my efforts have hitherto failed to demonstrate any segmentation in the mesoblast of the head, other than that indicated by the sections of the body-cavity before mentioned; but since these, as above stated, must be regarded as equivalent to muscle-plates, any further segmentation of mesoblast could not be anticipated. To this statement the posterior part of the head forms an apparent exception. Not far behind the auditory involution there are visible at the end of period K a few longitudinal muscles, forming about three or four muscle-plates, the ventral part of which is wanting. I have not the means of deciding whether they properly belong to the head, or may not really be a part of the trunk system of muscles which has, to a certain extent, overlapped the back part of the head, but am inclined to accept the latter view. These cranial muscle-plates are shewn in Pl. XIV. fig. 15 *b*, and in Pl. XVI. fig. 2.

Notochord in the Head.

The notochord during stage G is situated for its whole length

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[1] A report of the lectures appeared in *Nature*.

close under the brain, and terminates opposite the base of the mid-brain. As the cranial flexure becomes greater and mesoblast is collected in the angle formed by this, the termination of the notochord recedes from the base of the brain, but remains in close contact with the front end of the alimentary canal. At the same time its terminal part becomes very much thinner than the remainder, ends in a point, and exhibits signs of a retrogressive metamorphosis. It also becomes bent upon itself in a ventral direction through an angle of 180°; vide Pl. XIV. fig. 9 *a* and 16 *a*. In some cases this curvature is even more marked than is represented in these figures.

The bending of the end of the notochord is not directly caused by the cranial flexure, as is proved by the fact that the end of the notochord becomes bent through a far greater angle than does the brain. During the stages subsequent to K the ventral flexure of the notochord disappears, and its terminal part acquires by stage O a distinct dorsal curvature.

Hypoblast of the head.

The only feature of the alimentary tract in the head which presents any special interest is the formation of the gill-slits and of the thyroid body. In the present section the development of the former alone is dealt with: the latter body will be treated in the section devoted to the general development of the alimentary tract.

The gill-slits arise as outgrowths of the lining of the throat towards the external skin. In the gill-slits of Torpedo I have observed a very slight ingrowth of the external skin towards the hypoblastic outgrowth in one single case. In all other cases observed by me, the outgrowth from the throat meets the passive external skin, coalesces with it, and then, by the dissolution of the wall separating the lumen of the throat from the exterior, a free communication from the throat outwards is effected; vide Pl. XIV. fig. 5 *a* and *b*, and 13 *b*. Thus it happens that the walls lining the clefts are entirely formed of hypoblast. The clefts are formed successively[1], the anterior appearing first, and it is not till after the rudiments of three have appeared, that any of them become open to the exterior.

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[1] Vide Plates VI. and VII.

In stage K, four if not five are open to the exterior, and the rudiments of six, the full number, have appeared[1]. Towards the close of stage K there arise, from the walls of the 2nd, 3rd, and 4th clefts, very small knob-like processes, the rudiments of the external gills. These outgrowths are formed both by the lining of the gill-cleft and by the adjoining mesoblast[2].

From the mode of development of the gill-clefts, it appears that their walls are lined externally by hypoblast, and therefore that the external gills are processes of the walls of the alimentary tract, *i.e.* are covered by an hypoblastic, and not an epiblastic layer. It should be remembered, however, that after the gill-slits become open, the point where the hypoblast joins the epiblast ceases to be determinable, so that some doubt hangs over the above statement.

The identification of the layer to which the gills belong is not without interest. If the external gills have an epiblastic origin, they may be reasonably regarded[3] as homologous with the external gills of Annelids; but, if derived from the hypoblast, this view becomes, to say the least, very much less probable.

Segmentation of the Head.

The nature of the vertebrate head and its relation to the trunk forms some of the oldest questions of Philosophical Morphology.

The answers of the older anatomists to these questions are of a contradictory character, but within the last few years it has been more or less generally accepted that the head is, in part at least, merely a modified portion of the trunk, and composed, like that, of a series of homodynamous segments[4]. While the researches of Huxley, Parker, Gegenbaur, Götte, and other anatomists, have demonstrated in an approximately conclusive manner that the head is composed of a series of segments, great divergence of opinion still exists both as to the number of these segments, and

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[1] The description of stage K and L, pp. 77 and 78, is a little inaccurate with reference to the number of the visceral clefts, though the number visible in the hardened embryos is correctly described.

[2] Vide on the development of the gills, Schenk, *Sitz. d. k. Akad. Wien*, Vol. LXXI., 1875.

[3] Vide Dohrn, *Ursprung d. Wirbelthiere.*

[4] Semper, in his most recent work, maintains, if I understand him rightly, that the head is in no sense a modified part of the trunk, but admits that it is segmented in a similar fashion to the trunk.

as to the modifications which they have undergone, especially in the anterior part of the head. The questions involved are amongst the most difficult in the whole range of morphology, and the investigations recorded in the preceding pages do not, I am very well aware, go far towards definitely solving them. At the same time my observations on the nerves and on the head-cavities appear to me to throw a somewhat new light upon these questions, and it has therefore appeared to me worth while shortly to state the results to which a consideration of these organs points. There are three sets of organs, whose development has been worked out, each of which presents more or less markedly a segmental arrangement:—(1) The cranial nerves; (2) the visceral clefts; (3) the divisions of the head-cavity.

The first and second of these have often been employed in the solution of the present problem, while the third, so far as is known, exists only in the embryos of Elasmobranchs.

The development of the cranial nerves has recently been studied with great care by Dr Götte, and his investigations have led him to adopt very definite views on the segments of head. The arrangement of the cranial nerves *in the adult* has frequently been used in morphological investigations about the skull, but there are to my mind strong grounds against regarding it as affording a safe basis for speculation. The most important of these depends on the fact that nerves are liable to the greatest modification on any changes taking place in the organs they supply. On this account it is a matter of great difficulty, amounting in many cases to actual impossibility, to determine the morphological significance of the different nerve-branches, or the nature of the fusions and separations which have taken place at the roots of the nerves. It is, in fact, only in those parts of the head which have, relatively speaking, undergone but slight modifications, and which require no special elucidation from the nerves, that these sufficiently retain in the adult their primitive form to serve as trustworthy morphological guides.

I propose to examine separately the light thrown on the segmentation of the head by the development of (1) the nerves, (2) the visceral clefts, (3) the head-cavities; and then to compare the three sets of results so obtained.

The post-auditory nerves present no difficulties; they are all organized in the same fashion, and, as was first pointed out by

Gegenbaur, form five separate nerves, each indicating a segment. A comparison of the post-auditory nerves of Scyllium and other typical Elasmobranchs with those of Hexanchus and Heptanchus proves, however, that other segments were originally present behind those now found in the more typical forms. And the presence in Scyllium of numerous (twelve) strands from the brain to form the vagus, as well as the fact that a large section of the commissure connecting the vagus roots with the posterior roots of the spinal nerves is not connected with the brain, appear to me to shew that all traces of the lost nerves have not yet vanished.

Passing forwards from the post-auditory nerves, we come to the seventh and auditory nerves. The embryological evidence brought forward in this paper is against regarding these nerves as representing two segments. Although it must be granted that my evidence is not conclusive against an independent formation of these two nerves, yet it certainly tells in favour of their originating from a common rudiment, and Marshall's results on the origin of the two nerves in Birds (published in the *Journal of Anatomy and Physiology*, Vol. XI. Part 3) support, I have reason to believe, the same conclusion. Even were it eventually to be proved that the auditory nerve originated independently of the seventh, the general relations of this nerve, embryological and otherwise, are such that, provisionally at least, it could not be regarded as belonging to the same category as the facial or glossopharyngeal nerves, and it has therefore no place in a discussion on the segmentation of the head.

The seventh nerve of the embryo (Pl. XVI. fig. 1, VII.) is formed by the junction of three conspicuous branches, (1) an anterior dorsal branch which takes a more or less horizontal course above the eye (VII. *a*); (2) a main branch to the hyoid arch (VII. *hy*); (3) a smaller branch to the posterior edge of the mandibular arch (VII. *mn*). The first of these branches can clearly be nothing else but the typical "ramus dorsalis," of which however the auditory may perhaps be a specialized part. The fact that this branch pursues an anterior and not a directly dorsal course is probably to be explained as a consequence of the cranial flexure. The two other branches of the seventh nerve are the same as those present in all the posterior nerves, viz. the branches to the two sides of a branchial cleft, in the present instance the spiracle; the seventh nerve being clearly the nerve of the hyoid arch.

The fifth nerve presents in the arrangement of its branches a similarity to the seventh nerve so striking that it cannot be overlooked. This similarity is at once obvious from an inspection of the diagram of the nerves on Pl. XVI. fig. 1, V., or from an examination of the sections representing these nerves (Pl. XVI. figs. 3 and 4). It divides like the seventh nerve into three main branches: (1) an anterior and dorsal branch (*r.* ophthalmicus profundus), whose course lies parallel to but ventral to that of the dorsal branch of the seventh nerve; (2) a main branch to the mandibular arch (*r.* maxillæ inferioris); and (3) an anterior branch to the palatine arcade (*r.* maxillæ superioris). I was at first inclined to regard the anterior branch of the fifth (ophthalmic) as representing a separate nerve, and was supported in this view by its relation to the most anterior of the head-cavities; but the unexpected discovery of an exactly *similar branch* in the seventh nerve has induced me to modify this view, and I am now constrained to view the fifth as a single nerve, whose branches exactly correspond with those of the seventh. The anterior branch of the fifth is, like the corresponding branch of the seventh, the *ramus dorsalis*, and the two other branches are the equivalent of the branches of the seventh, which fork over the spiracle, though in the case of the fifth nerve no distinct cleft is present unless we regard the mouth as such. Embryology thus appears to teach us that the fifth nerve is a single nerve supplying the mandibular arch, and not, as has been usually thought, a complex nerve resulting from the coalescence of two or three distinct nerves. My observations do not embrace the origin or history of the third, fourth, and sixth nerves, but it is hardly possible to help suspecting that in these we have the nerve of one or more segments in front of that supplied by the fifth nerve; a view which well accords with the most recent morphological speculations of Professor Huxley[1].

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[1] Preliminary note upon the brain and skull of Amphioxus, *Proc. of the Royal Society*, Vol. XXII.

From this enumeration of the nerves the optic nerve is excluded for obvious reasons, and although it has been shewn above that the olfactory nerve developes like the other nerves as an outgrowth from the brain, yet its very late appearance and peculiar relations are, at least for the present, to my mind sufficient grounds for excluding it from the category of segmental cranial nerves.

The nerves then give us indications of seven cranial segments, or, if the nerves to the eye-muscles be included, of *at the least* eight segments, but to these must be added a number of segments now lost, but which once existed behind the last of those at present remaining.

The branchial clefts have been regarded as guides to segmentation by Gegenbaur, Huxley, Semper, etc., and this view cannot I think be controverted. In Scyllium there are six clefts which give indications of seven segments, viz. the segments of the mandibular arch, hyoid arch, and of the five branchial arches. If, following the views of Dr Dohrn[1], we regard the mouth as representing a cleft, we shall have seven clefts and eight segments; and it is possible, as pointed out in Dr Dohrn's very suggestive pamphlet, that remnants of a still greater number of præoral clefts may still be in existence. Whatever may be the value of these speculations, such forms as Hexanchus and Heptanchus and Amphioxus make it all but certain that the ancestors of Vertebrates had a number of clefts behind those now developed.

The last group of organs to be dealt with for our present question is that of the Head-Cavities.

The walls of the spaces formed by cephalic prolongations of the body-cavity develope into muscles and resemble the muscle-plates of the trunk, and with these they must be identified, as has been already stated. As equivalent to the muscle-plates, they clearly are capable of serving as very valuable guides for determining the segmentation of the head. There are then a pair of these in front of the mandibular arch, a pair in the mandibular arch, and a pair in each succeeding arch. In all there are eight pairs of these cavities representing eight segments, the first of them præoral. As was mentioned above, each of the sections of the head-cavity (except perhaps the

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[1] *Ursprung d. Wirbelthiere.*

first) stands in a definite relation to the nerve and artery of the arch in which it is situated.

The comparative results of these three independent methods of determining the segmentation of the head are in the subjoined table represented in a form in which they can be compared:—

Table of the Cephalic Segments as determined by the Nerves, Visceral Arches, and Head-Cavities.

Segments.	Nerves.	Visceral Arches.	Head-Cavities or Cranial Muscle-Plates.
Præoral 1	3rd and 4th and ? 6th nerves (perhaps representing more than one segment)	(?)	1st head-cavity (in my figures 1 *pp.*)
Postoral 2	5th nerve	Mandibular	2nd head-cavity (in my figures 2 *pp.*)
—— 3	7th nerve	Hyoid	3rd head-cavity
—— 4	Glossopharyngeal nerve	1st branchial arch	4th head-cavity
—— 5	1st branch of vagus	2nd branchial arch	5th head-cavity
—— 6	2nd branch of vagus	3rd branchial arch	6th head-cavity
—— 7	3rd branch of vagus	4th branchial arch	7th head-cavity
—— 8	4th branch of vagus	5th branchial arch	8th head-cavity

In the above table the first column denotes the segments of the head as indicated by a comparison of the three sets of organs employed. The second column denotes the segments as obtained by an examination of the nerves; the third column is for the visceral arches (which lead to the same results as, but are more convenient for our table than, the visceral clefts), and the fourth column is for the head-cavities. It may be noticed that from the second segment backwards the three sets of organs lead to the same results. The head-cavities indicate one segment in front of the mouth, and now that the ophthalmic branch of the fifth has been dethroned from its position as a separate nerve, the eye-nerves, or one of them, may probably be regarded as belonging to this segment. If the suggestion made above (p. 208), that the walls of the first cavity become the eye-muscles, be correct, the eye-nerves would perhaps after all be the most suitable nerves to regard as belonging to the segment of the first head-cavity.

CHAPTER X.

THE ALIMENTARY CANAL.

THE present Chapter completes the history of the primitive alimentary canal, whose formation has already been described. In order to economise space, no attempt has been made to give a full account of the alimentary canal and its appendages, but only those points have been dealt with which present any features of special interest.

The development of the following organs is described in order.

(1) The solid œsophagus.
(2) The postanal section of the alimentary tract.
(3) The cloaca and anus.
(4) The thyroid body.
(5) The pancreas.
(6) The liver.
(7) The subnotochordal rod.

The solid œsophagus.

A curious point which has turned up in the course of my investigations is the fact that for a considerable period of embryonic life a part of the œsophagus remains quite solid and without a lumen. The part of the œsophagus to undergo this peculiar change is that which overlies the heart, and extends from the front end of the stomach to the branchial region. At first, this part of the œsophagus has the form of a tube with a well-developed lumen like the remainder of the alimentary tract, but at a stage slightly younger than K its lumen becomes smaller, and finally vanishes, and the original tube is replaced by a solid rod of uniform and somewhat polygonal cells. A section of it in this condition is represented in Pl. x. fig. 8*a*.

At a slightly later stage its outermost cells become more columnar than the remainder, and between stages K and L it loses its cylindrical form and becomes much more flattened. By stage L the external layer of columnar cells is more definitely established, and the central rounded cells are no longer so numerous (Pl. XVII. fig. 4, *s œs.*).

In the succeeding stages the solid part of the œsophagus immediately adjoining the stomach is carried farther back relatively to the heart and overlies the front end of the liver. A lumen is not however formed in it by the close of stage Q, and beyond that period I have not carried my investigations, and cannot therefore state the exact period at which the lumen reappears. The limits of the solid part of the œsophagus are very satisfactorily shewn in longitudinal and vertical sections.

The solidification of the œsophagus belongs to a class of embryological phenomena which are curious rather than interesting, and are mainly worth recording from the possibility of their turning out to have some unsuspected morphological bearings.

Up to stage Q there are no signs of a rudimentary air-bladder.

The postanal section of the alimentary tract.

An account has already been given (p. 91) of the posterior continuity of the neural and alimentary canals, and it was there stated that Kowalevsky was the discoverer of this peculiar arrangement. Since that account was published, Kowalevsky has given further details of his investigations on this point, and more especially describes the later history of the hindermost section of the alimentary tract. He says[1]:

> The two germinal layers, epiblast and hypoblast, are continuous with each other at the border of the germinal disc. The primitive groove or furrow appears at the border of the germinal disc and is continued from the upper to the lower side. By the closing of the groove there is formed the medullary canal above, while the part of the groove on the under surface directed below is chiefly converted into the hind end of the alimentary tract. The connection of the two tubes in Acanthias persists till the formation of the anus, and the part of the nervous tube which lies under the chorda passes

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[1] *Archiv f. Mic. Anat.* Vol. XIII. pp. 194, 195.

gradually upwards to the dorsal side of the chorda, and persists there for a long time in the form of a large thin-walled vesicle.

The last part of the description beginning at "The connection of" does not hold good for any of the genera which I have had an opportunity of investigating, as will appear from the sequel.

In a previous section[1] the history of the alimentary tract was completed up to stage G.

In stage H the point where the anus will (at a very much later period) appear, becomes marked out by the alimentary tract sending down a papilliform process towards the skin. This is shewn in Pl. VI. figs. *H* and *I*, *an.*

That part of the alimentary tract which is situated behind this point may, for convenience, be called *the postanal section.* During stage H the postanal section begins to develope a terminal dilatation or vesicle, connected with the remainder of the canal by a narrower stalk. The relation in diameter between the vesicle and the stalk may be gathered by a comparison of fig. 3*a* and 3*b*, Pl. X. The diameter of the vesicle represented in section in Pl. X. fig. 3, is 0·328 Mm.

The walls both of the vesicle and stalk are formed of a fairly columnar epithelium. The vesicle communicates in front by a narrow passage (Pl. X. fig. 3*a*) with the neural canal, and behind is continued into two horns (Pl. X. fig. 2, *al.*) corresponding with the two caudal swellings spoken of above (p. 73). Where the canal is continued into these two horns, its walls lose their distinctness of outline, and become continuous with the adjacent mesoblast.

In the succeeding stages up to K the tail grows longer and longer, and with it grows the postanal section of the alimentary tract, without however altering in any of its essential characters.

Its features at stage K are illustrated by an optical section of the tail of an embryo (Pl. XVII. fig. 5) and by a series of transverse sections through the tail of another embryo in Pl. XVII. fig. 6*a*, 6*b*, 6*c*, 6*d*. In the optical section there is seen a terminal vesicle (*alv*) opening into the neural canal, and con-

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[1] p. 87 et seq.

nected with the remainder of the alimentary tract. The terminal vesicle causes the end of the tail to be dilated, as is shewn in Pl. VII. fig. *K*. The length of the postanal section extending from the abdominal paired fins to the end of the tail (equal to rather less than one-third of the whole length of the embryo), may be gathered from the same figure.

The most accurate method of studying this part of the alimentary canal is by means of transverse sections. Four sections have been selected for illustration (Pl. XVII. fig. 6*a*, 6*b*, 6*c*, and 6*d*) out of a fairly-complete series of about one hundred and twenty.

Posteriorly (fig. 6*a*) there is present a terminal vesicle ·25 Mm. in diameter, and therefore rather smaller than in the earlier stage, whose walls are formed of columnar epithelium, and which communicates dorsally by a narrow opening with the neural canal; to this is attached a stalk in the form of a tube, also lined by columnar epithelium, and extending through about thirty sections (Pl. XVII. fig. 6*b*). Its average diameter is about ·084 Mm. Overlying its front end is the subnotochordal rod (fig. 6*b*, *x*.), but this does not extend as far back as the terminal vesicle.

The thick-walled stalk of the vesicle is connected with the cloacal section of the alimentary tract by a very narrow thin-walled tube (Pl. XVII. 6*c*, *al*.). This for the most part has a fairly uniform calibre, and a diameter of not more than ·035 Mm. Its walls are formed of a flattened epithelium. At a point not far from the cloaca it becomes smaller, and its diameter falls to ·03 Mm. In front of this point it rapidly dilates again, and, after becoming fairly wide, opens on the dorsal side of the cloacal section of the alimentary canal just behind the anus (fig. 6*d*).

Near the close of stage K at a point shortly behind the anus, where the postanal section of the canal was thinnest in the early part of the stage, the alimentary canal becomes solid (Pl. XI. fig. 9*d*), and a rupture here occurs in it at a slightly later period.

In stage L the posterior part of the postanal section of the canal is represented by a small rudiment near the end of the tail. The rudiment no longer has a terminal vesicle, *nor does* *it communicate with the neural canal.* It was visible in one series for about 40 sections, and was continued forwards by a few granular cells, lying between the aorta and the caudal vein. The portion of the postanal section of the alimentary tract just behind the cloaca, was in the same embryo represented by a still smaller rudiment of the dilated part which at an earlier period opened into the cloaca.

Later than stage L no trace of the postanal section of the alimentary canal has come under my notice, and I conclude that it vanishes without becoming converted into any organ in the adult. Since my preliminary account of the development of Elasmobranch Fishes was written, no fresh light appears to have been thrown on the question of the postanal section of the alimentary canal being represented in higher Vertebrata by the allantois.

The cloaca and anus.

Elasmobranchs agree closely with other Vertebrates in the formation of the cloaca and anus, and in the relations of the cloaca to the urinogenital ducts.

The point where the anus, or more precisely the external opening of the cloaca, will be formed, becomes very early marked out by the approximation of the wall of the alimentary tract and external skin. This is shewn for stages H and I in Pl. VI. *an.*

Between stages I and K the alimentary canal on either side of this point, which we may for brevity speak of as the anus, is far removed from the external skin, but at the anus itself the lining of the alimentary canal and the skin are in absolute contact. There is, however, no involution from the exterior, but, on the contrary, the position of the anus is marked by a distinct prominence. Opposite the anus the alimentary canal dilates and forms the cloaca.

During stage K, just in front of the prominence of the anus, a groove is formed between two downgrowths of the body-wall. This is shewn in Pl. XI. fig. 9*a*. During the same stage the segmental ducts grow downwards to the cloaca, and open into it in the succeeding stage (Pl. XI. fig. 9*b*). Up to stage K the cloaca is connected with the præanal section of the alimentary canal in front, and the postanal section behind; the latter, however, by stage L, as has been stated above, atrophies, with the exception of a very small rudiment. In stage L the posterior part of the cloaca is on a level with the hind end of the kidneys, and is situated behind the posterior horns of the body-cavity, which are continued backwards to about the point where the segmental ducts open into the cloaca, and though very small at their termination rapidly increase in size anteriorly.

Nothing very worthy of note takes place in connection with the cloaca till stage O. By this stage we have three important structures developed. (1) An involution from the exterior to form the mouth of the cloaca or anus. (2) A perforation leading into the cloaca at the hind end of this. (3) The rudiments of the abdominal pockets. All of these structures are shewn in Pl. XVIII. fig. 1*a*, 1*b*, 1*c*.

The mouth of the cloaca is formed by an involution of the skin, which is deepest in front and becomes very shallow behind (Pl. XVIII. fig. 1*a*, 1*b*). At first only the mucous layer of the skin takes part in it, but when the involution forms a true groove, both layers of the skin serve to line it. At its posterior part, where it is shallowest, there is present, at stage O, a slit-like longitudinal perforation, leading into the posterior part of the cloaca (Pl. XVIII. fig. 1*c*) and forming its external opening. Elsewhere the wall of the cloaca and cloacal groove are merely in contact but do not communicate. On each side of the external opening of the cloaca there is present an involution (Pl. XVIII. fig. 1*c*, *ab. p.*) of the skin, which resembles the median cloacal involution, and forms the rudiment of an abdominal pocket. These two rudiments must not be confused with two similar ones, which are present in all the three sections represented, and mark out the line which separates the limbs from the trunk. These latter are not present in the succeeding stages. The abdominal pockets are only found in sections through the opening into the cloaca, and are only visible in the hindermost of my three sections.

All the structures of the adult cloaca appear to be already constituted by stage O, and the subsequent changes, so far as I have investigated them, may be dealt with in very few words. The perforation of the cloacal involution is carried slowly forwards, so that the opening into the cloaca, though retaining its slit-like character, becomes continuously longer; by stage Q its size is very considerable. The cloacal involution, relatively to the cloaca, recedes backwards. In stage O its anterior end is situated some distance in front of the opening of the segmental duct into the cloaca; by stage P the front end of the cloacal involution is nearly opposite this opening, and by stage Q is situated behind it.

As I have shewn elsewhere[1], the so-called abdominal pores of Scyllium are simple pockets open to the exterior, but without any communication with the body-cavity. By stage Q they are considerably deeper than in stage O, and retain their original position near the hind end of the opening into the cloaca. The opening of the urinogenital ducts into the cloaca will be described in the section devoted to the urinogenital system.

In Elasmobranchs, as in other Vertebrata, that part of the cloaca which receives the urinogenital ducts, is in reality the hindermost section of the gut and not the involution of epiblast which eventually meets this. Thus the urinogenital ducts at first open into the alimentary canal and not to the exterior. This fact is certainly surprising, and its meaning is not quite clear to me.

The very late appearance of the anus may be noticed as a point in which Elasmobranchs agree with other Vertebrata, notably the Fowl[2]. The abdominal pockets, as might be anticipated from their structure in the adult, are simple involutions of the epiblast.

The thyroid body.

The earliest trace of the thyroid body has come under my notice in a Torpedo embryo slightly older than I. In this embryo it appeared as a diverticulum from the ventral surface of the throat in the region of the *mandibular arch*, and extended from the border of the mouth to the point where the ventral aorta divided into the two aortic branches of the mandibular

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[1] *This Journal*, Vol. x. p. 34.

[2] Vide Gasser, *Entwicklungsgeschichte der Allantois, etc.*

arch. In front it bounded a groove (Pl. XIV. fig. 5*a*, *Th.*), directly continuous with the narrow posterior pointed end of the mouth and open to the throat, while behind it became a solid rod attached to the ventral wall of the œsophagus (Pl. XIV. fig. 5*b*, *Th.*). In a Scyllium embryo belonging to the early part of stage K, the thyroid gland presented the same arrangement as in the Torpedo embryo just described, with the exception that no solid posterior section of it was present.

Towards the close of stage K the thyroid body begins to elongate and become solid, though it still retains its attachment to the wall of the œsophagus. The solidification is effected by the columnar cells which line the groove elongating and meeting in the centre. As soon as the lumen is by these means obliterated, small cells make their appearance in the interior of the body, probably budded off from the original columnar cells.

The gland continues to grow in length, and by stage L assumes a long sack-like form with a layer of columnar cells bounding it externally, and a core of rounded cells filling up its interior. Anteriorly it is still attached to the throat, and its posterior extremity lies immediately below the end of the ventral aorta. The cells of the gland contain numerous yellowish concretionary pigment bodies, which are also present in the later stages.

Up to stage P the thyroid gland retains its original position. Its form and situation are shewn in Pl. XVIII. fig. 3, *th.*, in longitudinal and vertical section for a stage between O and P. The external layer of columnar cells has now vanished, and the gland is divided up by the ingrowth of connective-tissue septa into a number of areas or lobules—the rudiments of the future follicles. These lobules are perfectly solid without any trace of a lumen. A capillary network following the septa is present.

By stage Q the rudimentary follicles are more distinctly marked, but still without a lumen, and a connective-tissue sheath indistinctly separated from the surrounding tissue has been formed. My sections do not shew a junction between the gland and the epithelium of the throat; but the two are so close together, that I am inclined to think that such a junction still exists. It is certainly present up to stage P.

Dr Müller[1], in his exhaustive memoir on the thyroid body, gives an account of its condition in two Acanthias embryos. In his earliest embryo (which, judging from the size, is perhaps about the same age as my latest) the thyroid body is disconnected from the throat, yet contains a lumen, and is not divided up into lobules. It is clear from this account, that there must be considerable differences of detail in the development of the thyroid body in Acanthias and Scyllium.

In the Bird Dr Müller's figures shew that the thyroid body developes in the region of the hyoid arch, whereas, in Elasmobranchs, it developes in the region of the mandibular arch. Dr Götte's[2] account of this body in Bombinator accords very completely with my own, both with reference to the region in which it developes, and its mode of development.

The pancreas.

The pancreas arises towards the close of stage K as a somewhat rounded hollow outgrowth from the dorsal side of that part of the gut which from its homologies may be called the duodenum. In the region where the pancreas is being formed the appearances presented in a series of transverse sections are somewhat complicated (Pl. XVII. fig. 1), owing to the several parts of the gut and its appendages which may appear in a single section, but I have detected no trace of other than a single outgrowth to form the pancreas.

By stage L the original outgrowth from the gut has become elongated longitudinally, but transversely compressed: at the same time its opening into the duodenum has become somewhat narrowed.

Owing to these changes the pancreas presents in longitudinal and vertical section a funnel-shaped appearance (Pl. XVIII. fig. 4). From the expanded dorsal part of the funnel, especially from its anterior end, numerous small tubular diverticula grow out into the mesoblast. The apex of the funnel leads into the duodenum. From this arrangement it results that at this period the original outgrowth from the duodenum serves as a receptacle into which each ductule of the embryonic gland opens

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[1] *Jenaische Zeitschrift*, Vol. VI.

[2] *Entwicklungsgeschichte d. Unke.*

separately. I have not followed in detail the further growth of the gland. It is, however, easy to note that while the ductules grow longer and become branched, vascular processes grow in between them, and the whole forms a compact glandular body in the mesentery on the dorsal side of the alimentary tract, and nearly on a level with the front end of the spiral valve. The funnel-shaped receptacle loses its original form, and elongating, assumes the character of a duct.

From the above account it follows that the glandular part of the pancreas, and not merely its duct, is derived from the original hypoblastic outgrowth from the gut. This point is extremely clear in my preparations, and does not, in spite of Schenk's observations to the contrary[1], appear to me seriously open to doubt.

The liver.

The liver arises during stage I as a ventral outgrowth from the duodenum immediately in front of the opening of the umbilical canal (duct of the yolk-sack) into the intestine. Almost as soon as it is formed this outgrowth developes two lateral diverticula opening into a median canal.

The two diverticula are the rudimentary lobes of the liver, and the median duct is the rudiment of the common bile-duct (ductus choledochus) and gall-bladder (Pl. XI. fig. 9).

By stage K the hepatic diverticula have begun to bud out a number of small hollow knobs. These rapidly increase in length and number, and form the so-called hepatic cylinders. They anastomose and unite together, so that by stage L there is constructed a regular network. As the cylinders increase in length their lumen becomes very small, but appears never to vanish (Pl. XVIII. fig. 5).

The mode of formation of the liver parenchyma by hollow and not solid outgrowths agrees with the suggestion made in the *Elements of Embryology*, p. 133, and also with the results of Götte on the Amphibian liver. Schenk has thrown doubts upon the hypoblastic nature of the secreting tissue of the liver, but it does not appear to me, from my own investigations, that this point is open to question.

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[1] *Lehrbuch d. vergleichenden Embryologie.*

Coincidently with the formation of the hepatic network, the umbilical vein (Pl. XI. fig. 9, *u. v.*) which unites with the subintestinal or splanchnic vein (Pl. X. fig. 8 *V.*) breaks up into a series of channels, which form a second network in the spaces of the hepatic network. These vascular channels of the liver appear to me to have from the first distinct walls of delicate spindle-shaped cells, and I have failed to find a stage similar to that described by Götte for Amphibians in which the blood-channels are simply lacunar spaces in the hepatic parenchyma.

The changes of the median duct of the liver are of rather a passive nature. By stage O its anterior end has dilated into a distinct gall-bladder, whose duct receives in succession the hepatic ducts, and so forms the ductus choledochus. The ductus choledochus opens on the ventral side of the intestine immediately in front of the commencement of the spiral valve.

It may be noted that the liver and pancreas are corresponding ventral and dorsal appendages of the part of the alimentary tract immediately in front of its junction with the yolk-sack.

The subnotochordal rod.

The existence of this remarkable body in Vertebrata was first made known by Dr Götte[1], who not only demonstrated its existence, but also gave a correct account of its development. Its presence in Elasmobranchs and mode of development were mentioned by myself in my preliminary account of the development of these fishes[2], and it has been independently observed and described by Professor Semper[3]. No plausible suggestion as to its function has hitherto been made, and it is therefore a matter of some difficulty to settle with what group of organs it ought to be treated. In the presence of this difficulty it seemed best to deal with it in this chapter, since it is unquestionably developed from the wall of the alimentary canal.

At its full growth this body forms a rod underlying the notochord, and has nearly the same longitudinal extension as

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[1] *Archiv für Micros. Anatomie*, Bd. v., and *Entwicklungsgeschichte d. Unke.*

[2] *Quarterly Journal of Microscopic Science*, Oct. 1874.

[3] *Stammverwandschaft d. Wirbelthiere u. Wirbellosen* and *Das Urogenitalsystem d. Plagiostomen, Arb. Zool. Zoot. Institut. z. Würzburg*, Bd. 11.

this. It is indicated in most of my sections by the letter x. We may distinguish two sections of it, the one situated in the head, the other in the trunk. The junction between the two occurs at the hind border of the visceral clefts.

The section in the trunk is the first to develope. It arises during stage H in the manner illustrated in Pl. X. figs. 1 and 1*a*. The wall of the alimentary canal becomes thickened (Pl. X. fig. 1) along the median dorsal line, or else produced into a ridge into which there penetrates a narrow prolongation of the lumen of the alimentary canal. In either case the cells at the extreme summit of the thickening become gradually constricted off as a rod, which lies immediately dorsal to the alimentary tract, and ventral to the notochord. The shape of the rod varies in the different regions of the body, but it is always more or less elliptical in section. Owing to its small size and soft structure it is easily distorted in the process of preparing sections.

In the hindermost part of the body its mode of formation differs somewhat from that above described. In this part the alimentary wall is very thick and undergoes no special growth prior to the formation of the subnotochordal rod; on the contrary, a small linear portion of the wall becomes scooped out along the median dorsal line, and eventually separates from the remainder as the rod in question. In the trunk the splitting off of the rod takes place from before backwards, so that the anterior part of it is formed before the posterior.

The section of the subnotochordal rod in the head would appear from my observations on Pristiurus to develope in the same way as in the trunk, and the splitting off from the throat proceeds from before backwards (Pl. XIV. fig. 4*a* x).

In Torpedo, this rod developes very much later in the head than in the trunk; and indeed my conclusion that it developes in the head at all is only based on grounds of analogy, since in my oldest Torpedo embryo (just younger than K) there is no trace of it present. In a Torpedo embryo of stage I the subnotochordal rod of the trunk terminated anteriorly by uniting with the wall of the throat. The junction was effected by a narrow pedicle, so that the rod appeared mushroom-shaped in section, the stalk representing the pedicle of attachment.

On the formation of the dorsal aorta, the subnotochordal rod becomes separated from the wall of the gut and the aorta interposed between the two.

The subnotochordal rod attains its fullest development during stage K. Anteriorly it terminates at a point well in front of the ear, though a little behind the end of the notochord; posteriorly it extends very nearly to the extremity of the tail and is almost co-extensive with the postanal section of the alimentary tract, though it does not quite reach so far back as the caudal vesicle (Pl. XVII. fig. 6 *b* *x*). In stage L it is still fairly large in the tail, though it has begun to atrophy anteriorly. We may therefore conclude that its atrophy, like its development, takes place from before backwards. In the succeeding stages I have failed to find any trace of it, and conclude, as does Professor Semper, that it disappears completely.

Götte[1] is of opinion that the subnotochordal rod is converted into the dorsal lymphatic trunk, and regards it as the anterior continuation of the postanal gut, which he believes to be also converted into a lymphatic trunk. My observations afford no support to these views, and the fact already mentioned, that the subnotochordal rod is nearly co-extensive with the postanal section of the gut, renders it improbable that both these structures are connected with the lymphatic system.

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[1] *Entwicklungsgeschichte d. Unke*, p. 775.

CHAPTER XI.

The Vascular System and Vascular Glands.

The present chapter deals with the early development of the heart, the development of the general circulatory system, especially the venous part of it, and the circulation of the yolk-sack. It also contains an account of two bodies which I shall call the suprarenal and interrenal bodies, which are generally described as vascular glands.

The heart.

The first trace of the heart becomes apparent during stage G, as a cavity between the splanchnic mesoblast and the wall of the gut immediately behind the region of the visceral clefts (Pl. x. fig. 4, *ht.*).

The body-cavity in the region of the heart is at first double, owing to the two divisions of it not having coalesced; but even in the earliest condition of the heart the layers of splanchnic mesoblast of the two sides have united so as to form a complete wall below. The cavity of the heart is circumscribed by a more or less complete epithelioid (endothelial) layer of flattened cells, connected with the splanchnic wall of the heart by protoplasmic processes. The origin of this lining layer I could not certainly determine, but its connection with the splanchnic mesoblast suggests that it is probably a derivative of this[1]. In front the cavity of the heart is bounded by the approximation of the splanchnic mesoblast to the wall of the throat, and behind by the stalk connecting the alimentary canal with the yolk-sack.

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[1] From observations on the development of the heart in the Fowl, I have been able to satisfy myself that the epithelioid lining of the heart is derived from the splanchnic mesoblast. When the cavity of the heart is being formed by the separation of the splanchnic mesoblast from the hypoblast, a layer of the former remains close to the hypoblast, but connected with the main mass of the splanchnic mesoblast by protoplasmic processes. A second layer next becomes split from the splanchnic mesoblast, connected with the first layer by the above-mentioned protoplasmic processes. These two layers form the epithelioid lining of the heart; between them is the cavity of the heart, which soon loses the protoplasmic trabeculæ which at first traverse it.

As development proceeds the ventral wall of the heart becomes bent inwards on each side on a level with the wall of the gut (Plate X. fig. 4), and eventually becomes so folded in as to form for the heart a complete muscular wall of splanchnic mesoblast. The growth inwards of the mesoblast to form the dorsal wall of the heart does not, as might be expected, begin in front and proceed backwards, but commences behind and is gradually carried forwards.

From the above account it is clear that I have failed to find in Elasmobranchs any traces of two distinct cavities coalescing to form the heart, such as have been recently described in Mammals and Birds; and this, as well as the other features of the formation of the heart in Elasmobranchs, are in very close accordance with the careful description given by Götte[1] of the formation of the heart in Bombinator. The divergence which appears to be indicated in the formation of so important an organ as the heart between Pisces and Amphibians on the one hand, and Aves and Mammalia on the other, is certainly startling, and demands a careful scrutiny. The most complete observations on the double formation of the heart in Mammalia have been made by Hensen, Götte and Kölliker. These observations lead to the conclusion (1) that the heart arises as two independent splits between the splanchnic mesoblast and the hypoblast, each with an epithelioid (endothelial) lining. (2) *That the heart is first formed at a period when the folding in of the splanchnopleure to form the throat has not commenced, and when therefore it would be impossible for it to be formed as a single tube.*

In Birds almost every investigator since von Baer has detected more or less clearly the coalescence of two halves to form the unpaired heart[2]. Most investigators have however believed that there was from the first an unpaired anterior section of the heart, and that only the posterior part was formed by the coalescence of two lateral halves. Professor

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[1] Bischoff has recently stated, *Historisch-kritische Bemerkungen ü. d. Entwickelung d. Säugethiereier*, that Götte has found a double formation of the heart in Bombinator. It may seem bold to question the accuracy of Bischoff's interpretation of writings in his own language, but I have certainly failed to gather this either from Dr Götte's text or figures.

[2] Vide *Elements of Embryology*, Foster and Balfour, pp. 64—66.

Darlste His, and more recently Kölliker, have stated that there is no such unpaired anterior section of the heart. My own recent observations confirm their conclusions as to the double formation of the heart, though I find that the heart has from the first a Λ-shaped form. At the apex of the Λ the two limbs are only separated by a median partition and are not continuous with the aortic arches, which do not arise till a later period[1]. In the Bird the heart arises just *behind* the completed throat, and a double formation of the heart appears in fact in all instances to be *most distinctly correlated with the non-closure of the throat,* a non-closure which it must be noted would render it impossible for the heart to arise otherwise than as a double cavity.

In the instances in which the heart arises as a double cavity *it is formed before the complete closure of the throat,* and in those in which it arises as a single cavity *it is formed subsequently to the complete formation of the throat.* There is thus a double coincidence which renders the conclusion almost certain, *that the formation of the heart as two cavities is a secondary change which has been brought about by variations in the period of the closing in of the wall of the throat.*

If the closing in of the throat were deferred and yet the primitive time of formation of the heart retained, it is clear that such a condition as may be observed in Birds and Mammals must occur, and that the two halves of the heart must be formed widely apart, and only eventually united on the folding in of the wall of the throat. We may then safely conclude that the double formation of the heart has no morphological significance, and does not, as might at first sight be supposed, imply that the ancestral Vertebrate had two tubes in the place of the present unpaired heart. I have spoken of this point at considerable length, on account of the morphological importance which has been attached to the double formation of the heart. But the views above enunciated are not expressed for the first time. In the *Elements of Embryology* we say, p. 64, "The

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[1] Professor Bischoff (*loc. cit.*) throws doubts upon the double formation of the heart, and supports his views by Dr Foster's and my failure to find any trace of a double formation of the heart in the chick. Professor Bischoff must I think have misunderstood our description, which contains a clear account of the double formation of the heart.

exact mode of development (of the heart) appears according to our present knowledge to be very different in different cases; and it seems probable that the differences are in fact the result of variations in the mode of formation and time of closure of the alimentary canal." Götte again in his great work[1] appears to maintain similar views, though I do not perfectly understand all his statements. In my review of Kölliker's Embryology[2] this point is still more distinctly enunciated in the following passage: "The primitive wide separation and complete independence of the two halves of the heart is certainly surprising; but we are inclined, provisionally at least, to regard it as a secondary condition due to the late period at which the closing of the throat takes place in Mammals."

The general circulation.

The chief points of interest in connection with the general circulation centre round the venous system. The arterial arches present no peculiarities: the dorsal aorta, as in all other Vertebrates, is at first double (Pl. x. fig. 6 *ao*), and, generally speaking, the arrangement of the arteries accords with what is already known in other forms. The evolution of the venous system deserves more attention.

The cardinal veins are comparatively late developments. There is at first one single primitive vein continuous in front with the heart and underlying the alimentary canal through its præanal and postanal sections. This vein is shewn in section in Pl. v. fig. 8, *V.* It may be called either the subintestinal or splanchnic vein. At the cloaca, where the gut enlarges and comes in contact with the skin, this vein is compelled to bifurcate (Pl. xvii. fig. 6 *d v. cau.*), and usually the two branches into which it divides are unequal in size. The two branches meet again behind the cloaca and take their course ventral to the postanal section of the gut and terminate close to the end of the tail, Pl. xvii. fig. 6 *c. v. cau.* In the tail they form what is usually known as the caudal vein. The venous system of

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[1] *Entwicklungsgeschichte d. Unke*, p. 779, 780, 781.
[2] *Journal of Anatomy and Physiology*, Vol. x. p. 794.

Scyllium or Pristiurus, during the early parts of stage K, presents the simple constitution just described.

Before proceeding to describe the subsequent changes which take place in it, it appears to me worth pointing out the remarkable resemblance which the vascular system of an Elasmobranch presents at this stage to that of an ordinary Annelid and Amphioxus. It consists, as does the circulatory system, in Annelids, of a neural vessel (the aorta) and an intestinal vessel, the blood flowing backwards in the latter and forwards in the former. The two in Elasmobranchs communicate posteriorly by a capillary system, and in front by the arterial arches, connected like the similar vessels in Annelids with the branchiæ. Striking as is this resemblance, there is a still closer resemblance between the circulation of the Scyllium embryo at stage K and that of Amphioxus. The two systems are in fact identical except in very small details. The subintestinal vessel, absent or only represented by the caudal vein and in part by the ductus venosus in higher Vertebrates and adult Fish, forms the main and only posterior venous trunk of Amphioxus and the embryo Scyllium. The only noteworthy point of difference between Amphioxus and the embryo Scyllium is the presence of a portal circulation in the former, absent at this stage in the latter; but even this is acquired in Scyllium before the close of stage K, and does not therefore represent a real difference between the two types.

The cardinal veins make their appearance before the close of stage K, and very soon unite behind with the unpaired section of the caudal vein (Pl. XI. fig. 9 *b*, *p. cav.* and *v.*). On this junction being effected retrogressive changes take place in the original subintestinal vessel. It breaks up in front into a number of smaller vessels; the lesser of the two branches connecting it round the cloaca with the caudal vein first vanishes (Pl. XI. fig. 9 *a*, *v*), and then the larger; and the two cardinals are left as the sole forward continuations of the caudal vein. This latter then becomes prolonged forwards, and the two posterior cardinals open into it some little distance in front of the hind end of the kidneys. By these changes and by the disappearance of the postanal section of the gut the caudal vein is made to appear as a superintestinal and not a subintestinal vessel, and as the direct posterior continuation of the cardinal veins. Embryology proves however that the caudal vein is a true subintestinal vessel[1], and that its connection with the cardinals is entirely secondary.

The invariably late appearance of the cardinal veins in the embryo and their absence in Amphioxus leads me to regard them as additions to the circulatory system which appeared in the Vertebrata themselves, and were not inherited from their ancestors. It would no doubt be easy to point to vessels in existing Annelids which might be regarded as their equivalent, but to do so would be in my opinion to follow an entirely false morphological scent.

The circulation of the yolk-sack.

The observations recorded on this subject are so far as I am acquainted with them very imperfect, and in most cases the arteries and veins appear to have been transposed.

Professor Wyman[2], however, gives a short description of the circulation in Raja Batis, in which he rightly identifies the arteries, though he regards the arterial ring which surrounds the vascular area as equivalent to the venous sinus terminalis of the Bird.

The general features of the circulation are clearly portrayed in the somewhat diagrammatic figures on Plate VIII., in which the arteries are represented red, and the veins blue[3].

I shall follow the figures on this plate in my descriptions.

Fig. 1 represents my earliest stage of the circulation of the yolk-sack. At this stage there is visible a single aortic trunk passing forwards from the embryo and dividing into two branches. No venous trunk could be detected with the simple microscope, but probably venous channels were present in the thickened edge of the blastoderm.

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[1] The morphological importance of this point is considerable. It proves, for instance, that the hæmal arches of the vertebræ in the tail (vide pp. 152 and 153) potentially, at any rate, encircle the gut and enclose the body-cavity as completely as ribs which meet in the median ventral line may be said to do anteriorly.

[2] *Memoirs of the American Academy of Arts and Sciences*, Vol. IX.

[3] I may state that my determinations of the arrangement of the circulation were made by actual observation of the flow of the blood under the microscope.

In fig. 2 the circulation was greatly advanced[1]. The blastoderm has now nearly completely enveloped the yolk, and there remains only a small circular space (*yk*) not enclosed by it. The arterial trunk is present as before, and divides in front of the embryo into two branches which turn backwards and nearly form a complete ring round the embryo. In general appearance it resembles the sinus terminalis of the area vasculosa of the Bird, but in reality bears quite a different relation to the circulation. It gives off branches only on its inner side.

A venous system of returning vessels is now fully developed, and its relations are very remarkable. There is a main venous ring round the thickened edge of the blastoderm, which is connected with the embryo by a single stem which runs along the seam where the edges of the blastoderm have coalesced. Since the venous trunks are only developed behind the embryo, it is only the posterior part of the arterial ring which gives off branches.

The succeeding stage, fig. 3, is also one of considerable interest. The arterial ring has greatly extended, and now embraces nearly half the yolk, and sends off trunks on its inner side along its whole circumference.

More important changes have taken place in the venous system. The blastoderm has now completely enveloped the yolk, and as a result of this, the venous ring no longer exists, but at the point where it vanished there may be observed a number of smaller veins diverging in a brush-like fashion from the termination of the unpaired trunk which originally connected the venous ring with the heart. This point is indicated in the figure by the letter *y*. The brush-like divergence of the veins is a still more marked feature in a blastoderm of a succeeding stage (fig. 4).

The circulation in the succeeding stage (fig. 4) (projected in my figure) only differs in details from that of the previous stage. The arterial ring has become much larger, and the portion of the yolk not embraced (*x*) by it is quite small.

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[1] My figure may be compared with that of Leydig, *Rochen und Haie*, Plate III. fig. 6. Leydig calls the arterial ring the sinus terminalis and appears to regard it as venous, but his description is so short that this point is not quite clear.

Instead of all the branches from the ring being of nearly equal size, two of them are especially developed. The venous system has undergone no important changes.

In fig. 5 the circulation is represented at a still later stage. The arterial ring has come to embrace the whole yolk, and as a result of this, has in its turn vanished as did the venous ring before it. At this stage of the circulation there is present a single arterial and a single venous trunk. The arterial trunk is a branch of the dorsal aorta, and the venous trunk originally falls into the heart together with the subintestinal or splanchnic vein, but on the formation of the liver enters this and breaks up into capillaries in it. The venous trunk leaves the body on the right side, and the arterial on the left.

The most interesting point to be noticed in connection with the yolk-sack circulation of Scyllium is the fact of its being formed on a completely different type to that of the Amniotic Vertebrates.

THE VASCULAR GLANDS.

There are in Scyllium two structures which have gone under the name of the suprarenal body. The one of these is an unpaired rod-like body lying between the dorsal aorta and the caudal vein in the region of the posterior end of the kidneys. This body I propose to call *the interrenal body.* The other is formed by a series of paired bodies situated dorsal to the cardinal veins on branches of the aorta, and arranged segmentally. These bodies I shall call *the suprarenal bodies.* I propose treating the literature of these bodies together, since they have usually been dealt with in this way, and indeed regarded as parts of the same system. As I hope to shew in the sequel, the origin of these bodies is very different. The interrenal body appears to be developed from the mesoblast; while my researches on the suprarenal bodies confirm the brilliant investigations of Leydig, shewing that they are formed out of the sympathetic ganglia.

The most important investigations on these bodies have been made by Leydig[1]. In his first researches, *Rochen u. Haie,*

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[1] *Rochen und Haie* and *Untersuchung. ü. Fische u. Reptilien.*

pp. 71, 72, he gives an account of the position and histology of what is probably my interrenal body[1].

The position and relations of the interrenal body vary somewhat according to Leydig in different cases. He makes the following statement about its histology. "Fat molecules form the chief mass of the body, which causes its white, or ochre-yellow colour, and one finds freely embedded in them clear vesicular nuclei." He then proceeds to state that this structure is totally dissimilar to that of the Mammalian suprarenal body, and gives it as his opinion that it is not the same body as this. In his later researches[2] he abandons this opinion, and adopts the view that the interrenal body is part of the same system as the suprarenal bodies to be subsequently spoken of. Leydig describes the suprarenal bodies as paired bodies segmentally arranged along the ventral side of the spinal column situated on the successive arteriæ axillares, and in close connection with one or more sympathetic ganglia. He finds them formed of lobes, consisting of closed vesicles full of nuclei and cells. Numerous nerve-fibres are also described as present. With reference to the real meaning of these bodies he expresses a distinct view. He says[3], "As the pituitary body is an integral part of the brain, so are the suprarenal bodies part of the sympathetic system." He re-affirms with still greater emphasis the same view in his *Fische u. Reptilien*. Though these views have not obtained much acceptance, and the accuracy of the histological data on which they are grounded has been questioned, yet I hope to shew in the sequel not only that Leydig's statements are in the main true, but that development proves his conclusions to have been well founded.

Stannius alludes[4] to both these bodies, and though he does

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[1] I do not feel sure that Leydig's unpaired suprarenal body is really my interrenal body, or at any rate it alone. The point could no doubt easily be settled with fresh specimens, but these I unfortunately cannot at present obtain. My doubts rest partly on the fact that, in addition to my interrenal body, other peculiar masses of tissue (which may be called lymphoid in lieu of a better name) are certainly present around some of the larger vessels of the kidneys which are not identical in structure and development with my interrenal body, and partly that Stannius' statements (to be alluded to directly) rather indicate the existence of a second unpaired body in connection with the kidneys, though I do not fully understand his descriptions.

[2] *Fische u. Reptilien*, p. 14.

[3] *Rochen u. Haie*, p. 18.

[4] *Vergleichende Anatomie*, II. Auflage.

not contribute much to Leydig's previous statements, yet he accepts Leydig's position with reference to the relation of the sympathetic and suprarenal bodies[1].

The general text-books of Histology, Kölliker's work, and Eberth's article in Stricker's *Histology*, do not give much information on this subject; but Eberth, without apparently having examined the point, questions the accuracy of Leydig's statements with reference to the anatomical relations of the sympathetic ganglia and suprarenal bodies.

The last author who has dealt with this subject is Professor Semper[2]. He records observations both on the anatomy and development of these organs. His anatomical observations are in the main confirmatory of those of Leydig, but he shews still more clearly than did Leydig the segmental arrangement of the suprarenal bodies. He definitely regards the interrenal and suprarenal bodies as parts of the same system, and states that in many forms they are continuous (p. 228):

"Hier freilich gehen sie bei manchen Formen...in einen Körper ueber, welcher zwischen den Enden d. beiden Nieren liegend dicht an der einfachen Caudalvene sitzt."

With reference to their development he says: "They arise then also completely independently of the kidneys, as isolated segmentally arranged groups of mesoderm cells between the convolutions of the segmental organs; only anteriorly do they stretch beyond them, and extend quite up to the pericardium."

To Semper's statements I shall return, but now pass on to my own observations. The paired suprarenal bodies are dealt with first.

The suprarenal bodies.

My observations on these bodies in the adult Scyllium have only been made with specimens hardened in chromic acid, and there are many points which deserve a fuller investigation than I have been able to give them.

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[1] Stannius' description is not quite intelligible, but appears to point to the existence of a third kind of body connected with the kidney. From my own observations (vide above), I am inclined to regard it as probable that such a third body exists.

[2] *Urogenitalsystem d. Plagiostomen. Arb. Zool. Zoot. Inst. z. Würzburg*, Vol. II.

The general position and relations of the suprarenal bodies have been fully given by Leydig and Semper, and I have nothing to add to their statements. They are situated on branches of the aorta, segmentally arranged, and extend on each side of the vertebral column from close behind the heart to the posterior part of the body-cavity. The anterior pair are the largest, and are formed apparently from the fusion of two bodies[1]. When these bodies are examined microscopically, their connection with the sympathetic ganglia becomes at once obvious. Bound up in the same sheath as the anterior one is an especially large ganglion already alluded to by Leydig, and sympathetic ganglia are more or less distinctly developed in connection with all the others. There is however considerable irregularity in the development and general arrangement of the sympathetic ganglia, which are broken up into a number of small ganglionic swellings, on some of which an occasional extra suprarenal body is at times developed. As a rule it may be stated that there is a much smaller ganglionic development in connection with the posterior suprarenal bodies than with the anterior.

The different suprarenal bodies exhibit variations in structure mainly dependent on the ganglion cells and nerves in them, and their typical structure is best exhibited in a posterior one, in which there is a comparatively small development of nervous elements.

A portion of a section through one of these is represented on Pl. XVIII. fig. 6, and presents the following features. Externally there is present a fibrous capsule, which sends in the septa, imperfectly dividing up the body into a series of alveoli or lobes. Penetrating and following the septa there is a rich capillary network. The parenchyma of the body itself exhibits a well-marked distinction in the majority of instances into a cortical and medullary substance. The cortical substance is formed of rather irregular columnar cells, for the most part one row deep, arranged round the periphery of the body. Its cells measure on about an average ·03 Mm. in their longest diameter. The medullary substance is more or less distinctly divided into

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[1] There is a very good figure of them in Semper's paper, Pl. XXI. fig. 3.

alveoli, and is formed of irregularly polygonal cells; and though it is difficult to give an estimate of their size on account of their irregularity, ·021 Mm. may be taken as probably about the diameter of an average cell. The character of the cortical and medullary cells is nearly the same, and the cells of the two strata appear rather to differ in shape than in any other essential point. The protoplasm of both has a markedly yellow tinge, giving to the suprarenal bodies a yellowish brown colour. The nuclei are small compared to the size of the cells, being about ·009 Mm. in both cortical and medullary cells. In the anterior suprarenal body there is a less marked distinction between the cortical and the medullary layers, and a less pronounced yellow coloration of the whole, than in the posterior bodies. The suprarenal bodies are often partially or completely surrounded by a lymphoid tissue, which is alluded to in the account of their development.

The most interesting features of my sections of the anterior bodies are the relations they bring to light between the sympathetic ganglia and the suprarenal bodies. In the case of one of the posterior suprarenal bodies, a small ganglion is generally found attached to both ends of the body, and invested in the same sheath; in addition to this a certain number of ganglion cells (very conspicuous by their size and other characters) are to be found scattered through the body. In the anterior suprarenal bodies the development of ganglion cells is very much greater. If a section is taken through the region where the large sympathetic ganglion (already mentioned) is attached to the body, one half of the section is composed mainly of sympathetic ganglion cells and nerve fibres, and the other of suprarenal tissue, but the former spread in considerable numbers into the latter. A transverse section through the suprarenal body in front of, or behind this point, is still more instructive. One of these is represented in Pl. XVIII. fig. 7. The suprarenal tissue is not inserted, but fills up the whole space within the outline of the body. At one point a nerve (*n*) is seen to enter. In connection with this are a number of ganglion cells, the exact distribution of which has been reproduced. They are scattered irregularly throughout the suprarenal body, but are more concentrated at the smaller than at the large end. It is this small end which, in succeeding sections, is entirely replaced by a sympathetic ganglion. Wavy fibres (which I take to be nervous) are distributed through the suprarenal body in a manner which, roughly speaking, is proportional to the number of ganglion cells. At the large end of the body, where there are few nerve cells, the typical suprarenal structure is more or less retained. Where the nerve fibres are more numerous at the small end of the section, they give to the tissue a somewhat peculiar appearance, though the individual suprarenal cells retain their normal structure. In a section of this kind the ganglion and nerves are clearly so intimately united with the suprarenal body as not to be separable from it.

The question naturally arises as to whether there are cells of an intermediate character between the ganglion cells and the cells of the suprarenal body. I have not clearly detected any such, but my observations are of too limited a character to settle the point in an adverse sense.

The embryological part of my researches on these bodies is in reality an investigation of later development of the sympathetic ganglia. The earliest stages in the development of these have already been given[1], and I take them up here as they appear during stage L, and shall confine my description to the changes they undergo in the anterior part of the trunk. They form during stage L irregular masses of cells with very conspicuous branches connecting them with the spinal nerves (Pl. XVII. fig. 3). There may be noticed at intervals solid rods of cells passing from the bodies to the aorta, Pl. XVII. fig. 2. These rods are the rudiments of the aortic branches to which the suprarenal bodies are eventually attached.

In a stage between M and N the trunks connecting these bodies with the spinal nerves are much smaller and less easy to see than during stage L. In some cases moreover the nerves appear to attach themselves more definitely to a central and inner part of the ganglia than to the whole of them. This is shewn in Pl. XVIII. fig. 8, and I regard it as the first trace of a division of the primitive ganglia into a suprarenal part and a ganglionic part. The branches from the aorta have now a

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[1] *Antea*, pp. 438, 439.

definite lumen, and take a course through the centre of these bodies, as do the aortic branches in the adult.

By stage O these bodies have acquired a distinct mesoblastic investment, which penetrates into their interior, and divides it, especially in the case of the anterior bodies, into a number of distinct alveoli. These alveoli are far more distinct in some parts of the bodies than in others. The nerve-trunks uniting the bodies with the spinal nerves are (at least in specimens hardened in picric and chromic acids) very difficult to see, and I have failed to detect that they are connected with special parts of the bodies, or that the separate alveoli differ much as to the nature of their constituent cells. The aortic branches to the bodies are larger than in the previous stage, and the bodies themselves fairly vascular.

By stage Q (Pl. XVIII. fig. 9) two distinct varieties of cells are present in these bodies. One of these is large, angular, and strikingly resembles the ganglion cells of the spinal nerves at the same period. This variety is found in separate lobules or alveoli on the inner border of the bodies. I take them to be true ganglion cells, though I have not seen them in my sections especially connected with the nerves. The cells of the second variety are also aggregated in special lobules, and are very markedly smaller than the ganglionic cells. They form, I imagine, the cells of the true suprarenal tissue. At this and the earlier stage lymphoid tissue, like that surrounding the suprarenal bodies in the adult, is found adjacent to these bodies.

Stage Q forms my last embryonic stage, and it may perhaps be asked on what grounds I regard these bodies as suprarenal bodies at all and not as simple sympathetic ganglia.

My determination mainly rests on three grounds: (1) That a branch from the aorta penetrates these bodies and maintains exactly the same relations to them that the same branches of the aorta do in the adult to the true suprarenal bodies. (2) That the bodies are highly vascular. (3) That in my last stage they become divided into a ganglionic and a non-ganglionic part, with the same relations as the ganglia and suprarenal tissue in the adult. These grounds appear to me to afford ample justification for my determinations, and the evidence adduced above appears to me to render it almost certain that the suprarenal tissue is a product of the primitive ganglion and not introduced from the mesoblast without, though it is not to be denied that a more complete investigation of this point than it has been possible for me to make would be very desirable.

Professor Semper states that he only made a very slight embryological investigation of these bodies, and probably has only carefully studied their later stages. He has accordingly overlooked the branches connecting them with the spinal nerves, and has not therefore detected the fact that they develope as parts of the sympathetic nervous system. I feel sure that if he re-examines his sections of younger embryos he will not fail to discover the nerve-branches described by me. His descriptions apart from this point accord fairly well with my own. The credit of the discovery that these bodies are really derivatives of the sympathetic nervous system is entirely Leydig's: my observations do no more than confirm his remarkable observations and well-founded conclusions.

Interrenal body.

My investigations on the interrenal body in the adult are even less complete than those on the suprarenal bodies. I find the body forming a small rod elliptical in section in the posterior region of the kidney between the dorsal aorta and unpaired caudal vein. Some little distance behind its front end (and probably not at its thickest point) it measured in one example, of which I have sections, a little less than a millimetre in its longest diameter. Anteriorly it overlaps the suprarenal bodies, and I failed to find any connection between them and it. On this point my observations do not accord with those of Professor Semper. I have however only been able to examine hardened specimens.

It is, vide Pl. XVII. fig. 8, invested by a fairly thick tunica propria, which sends in septa, dividing it into rather well-marked lobules or alveoli. These are filled with polygonal cells, which form the true parenchyma of the body. These cells are in my hardened specimens not conspicuous by the number of oil-globules they contain, as might have been expected from

Leydig's description[1]. They are rather granular in appearance, and are mainly peculiar from the somewhat large size of the nucleus. The diameter of an average cell is about ·015 Mm., and that of the nucleus about ·01 to ·012. The nuclei are remarkably granular. The septa of the body are provided with a fairly rich capillary network.

At the first glance there is some resemblance in structure between the tissues of the suprarenal and interrenal bodies, but on a closer inspection this resemblance resolves itself into both bodies being divided up into lobules by connective-tissue septa. There is in the interrenal body no distinction between cortical and medullary layers as in the suprarenal. The cells of the two bodies have very different characters, as is demonstrated by a comparison of the relative diameters of the nuclei and the cells. The cells of the suprarenal bodies are considerably larger than those of the interrenal (·021 to ·03 as compared to ·015), yet the nuclei of the larger cells of the former body do not equal in size those of the smaller cells of the latter (·009 as compared to ·01).

My observations both on the coarser anatomy and on the histology of the interrenal body in the adult point to its being in no way connected with the suprarenal bodies, and are thus in accordance with the earlier and not the later views of Leydig.

The embryology of this body (under the title of suprarenal body) was first described in my preliminary account of the development of the Elasmobranch Fishes[2]. A short account of its embryonic structure was given, and I stated that although I had not fully proved the point, yet I believed it to be derived from the wall of the alimentary canal. As will be shewn in the sequel this belief was ill-founded, and the organ in question is derived from the mesoblast. Allusion has also been made to it by Professor Semper, who figures it at an early stage of development, and implies that it arises in the

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[1] Perhaps the body I am describing is not identical with Leydig's posterior suprarenal body. I do not, as mentioned above, feel satisfied that it is so from Leydig's description.

[2] *Quarterly Journal of Microscopic Science*, October, 1874.

mesoblast and in connection with the suprarenal body. It appears at stage K as a rod-like aggregate of mesoblast cells, rather more closely packed than their neighbours, between the two kidneys near their hinder ends (Plate XI. fig. 9*a*, *su*). The posterior and best marked part of it does not extend further forwards than the front end of the large intestine, and reaches backwards nearly as far as the hinder end of the kidneys. This part of the body lies between the caudal vein and dorsal aorta.

At about the point where the unpaired caudal vein divides into the two cardinals, the interrenal body becomes less well marked off from the surrounding tissue, though it may be traced forward from a considerable distance in the region of the small intestine. It retains up to stage Q its original extension, but the anterior part becomes quite definite though still of a smaller calibre than the posterior. In one of my examples of stage O the two divisions were separated by a small interval, and not as in other cases continuous. I have not determined whether this was an accidental peculiarity or a general feature. I have never seen any signs of the interrenal body becoming continuous with the suprarenal bodies, though, as in the adult, the two bodies overlap for a considerable distance.

The histology of the interrenal body in the embryonic periods is very simple. At first it is formed of cells differing from those around in being more circular and more closely packed. By stage L its cells have acquired a character of their own. They are still spherical or oval, but have more protoplasm than before, and their nucleus becomes very granular. At the same time the whole body becomes invested by a tunic of spindle-shaped mesoblast cells. By stage O it begins to be divided into a number of separate areas or lobes by septa formed of nucleated fibres. These become more distinct in the succeeding stages up to Q (Pl. XVII. fig. 7), and in them a fair number of capillaries are formed.

From the above description it is clear that embryology lends no more countenance than does anatomy to the view that the interrenal bodies belong to the same system as the suprarenal, and it becomes a question with which (if of either) of these two bodies the suprarenal bodies of the higher Vertebrata are homologous. This question I shall not attempt to answer in a definite way. My own decided belief is that the suprarenal bodies of Scyllium are homologous with the suprarenal bodies of Mammalia, and a good many points both in their structure and position might be urged in favour of this view. In the mean time, however, it appears to me better to wait before expressing a definite opinion till the embryonic development of the suprarenal bodies has been worked out in the higher Vertebrata.

CHAPTER XII.

THE ORGANS OF EXCRETION.

THE earliest stages in the development of the excretory system have already been described in a previous chapter[1] of this memoir, and up to the present time no investigator, with the exception of Dr Alex. Schultz[2], has gone over the same ground. Dr Schultz' descriptions are somewhat brief, but differ from my own mainly in stating that the segmental duct arises from an involution instead of as a solid knob. This discrepancy is, I believe, due to Dr Schultz drawing his conclusions as to the development of the segmental duct from its appearance at a comparatively late stage. He appears to have been unacquainted with my earlier descriptions.

The adult anatomy and later stages in the development of the excretory organs form the subject of the present chapter, and stand in marked contrast to the earlier stages in that they have been dealt with in a magnificent monograph[3] by Professor Semper, whose investigations have converted this previously almost unknown field of vertebrate embryology into one of the most fully explored parts of the whole subject. Reference is frequently made to this monograph in the succeeding pages, but my references, numerous as they are, give no adequate idea of the completeness and thoroughness of Professor Semper's investigations. In Professor Semper's monograph are embodied the results of a considerable number of preliminary papers published by him in his *Arbeiten* and in the *Centralblatt.* The excretory organs of Elasmobranchs have also formed the subject of some

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[1] Chapter VI. p. 127, *et seq.*

[2] *Archiv f. Micr. Anat.* Bd. XI.

[3] *Urogenital System d. Plagiostomen,* Semper, *Arbeiten,* Vol. II.

investigations by Dr Meyer[1] and by myself[2]. Their older literature is fully given by Professor Semper. In addition to the above-cited works, there is one other paper by Dr Spengel[3] on the Urinogenital System of Amphibians, to which reference will frequently be made in the sequel, and which, though only indirectly connected with the subject of this chapter, deserves special mention both on account of the accuracy of the investigations of which it forms the record, and of the novel light which it throws on many of the problems of the constitution of the urinogenital system of Vertebrates.

Excretory organs and genital ducts in the adult.

The kidneys of Scyllium canicula are paired bodies in contact along the median line. They are situated on the dorsal wall of the abdominal cavity, and extend from close to the diaphragm to a point a short way behind the anus. Externally, each appears as a single gland, but by the arrangement of its ducts may be divided into two distinct parts, an anterior and a posterior. The former will be spoken of as the Wolffian body, and the latter as the kidney, from their respective homology with the glands so named in higher Vertebrates. The grounds for these determinations have already been fully dealt with both by Semper[4] and by myself.

Externally both the Wolffian body and the kidney are more or less clearly divided into segments, and though the breadth of both glands as viewed from the ventral surface is fairly uniform, yet the hinder part of the kidney is very much thicker and bulkier than the anterior part and than the whole of the Wolffian body. In both sexes the Wolffian body is rather longer than the kidney proper. Thus in a male example, 33 centimetres long, the two glands together measured 8¼ centimetres and the kidney proper only 3½. In the male the

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[1] *Sitzungsberichte d. Naturfor. Ges. Leipzig*, 1875. No. 2.

[2] Preliminary account of the development of Elasmobranch Fishes, *Quarterly Journal of Microscopical Science*, 1874. Origin and History of the Urinogenital organs of Vertebrates, *Journal of Anat. and Physiol.* Vol. x.

[3] *Arbeiten*, Semper, Vol. III.

[4] Though Professor Semper has come to the same conclusions as myself with respect to these homologies, yet he calls the Wolffian body Leydig's gland after its distinguished discoverer and its duct Leydig's duct.

Wolffian bodies extend somewhat further forwards than in the female. Leaving the finer details of the glands for subsequent treatment, I pass at once to their ducts. These differ slightly in the two sexes, so that it will be more convenient to take the male and female separately.

A partly diagrammatic representation of the kidney and Wolffian body of the male is given on Pl. XIX. fig. 1. The secretion of the Wolffian body is carried off by a duct, *the Wolffian duct* (*w.d.*), which lies on the ventral surface of the gland, and receives a separate ductule from each segment (Pl. XIX. fig. 5). The main function of the Wolffian duct in the male is, however, that of a vas deferens. The testicular products are brought to it through the coils of the anterior segments of the Wolffian body by a number of vasa efferentia, the arrangement of which is treated of on pp. 257, 258. The section of the Wolffian duct which overlies the Wolffian body is much contorted, and in adult individuals at the generative period enormously so. The duct often presents one or two contortions beyond the hind end of the Wolffian body, but in the normal condition takes a straight course from this point to the unpaired urinogenital cloaca, into which it falls independently of its fellow of the opposite side. It receives no feeders from the kidney proper.

The excretion of the kidney proper is carried off not by a single duct, but by a series of more or less independent ducts, which, in accordance with Prof. Semper's nomenclature, will be spoken of as *ureters*. These are very minute, and their investigation requires some care. I have reason, from my examinations of this and other species of Elasmobranchs, to believe that they are, moreover, subject to considerable variations, and the following description applies to a definite individual. Nine or possibly ten distinct ureters, whose arrangement is diagrammatically represented in fig. 1, Pl. XIX., were present on each side. It will be noticed that, whereas the five hindermost are distinct till close to their openings into the urinogenital cloaca, the four anterior ones appear to unite at once into a single duct, but are probably only bound up in a common sheath. The ureters fall into the common urinogenital cloaca, immediately behind the opening of the Wolffian duct (so far as could be determined), by four apertures on each side. In a section made through the part of the wall of the cloaca containing the openings of the ureters of both sides, there were present on the left side (where the section passed nearer to the surface than on the right) four small openings posteriorly, viz. the openings of the ureters and one larger one anteriorly, viz. the opening of the Wolffian duct. On the other side of the section where the level was rather deeper, there were five distinct ducts cut through, one of which was almost on the point of dividing into two. This second section proves that, in this instance at least, the two ureters did not unite till just before opening into the urinogenital cloaca. The same section also appeared to shew that one of the ureters fell not into the cloaca but into the Wolffian duct.

As stated above both the Wolffian duct and the ureters fall into an unpaired urinogenital cloaca. This cloaca communicates at one end with the general cloaca by a single aperture situated at the point of a somewhat conspicuous papilla, just behind the anus (Pl. XIX. fig. 1, *o*), and on the other it opens freely into a pair of bladders, situated in close contact with each other, on the ventral side of the kidney (Pl. XIX. fig. 1, *sb*). To these bladders Professor Semper has given the name *uterus masculinus*, from having supposed them to correspond with the lower part of the oviducts of the female. This homology he now admits to be erroneous, and it will accordingly be better to drop the name uterus masculinus, for which may be substituted *seminal bladder*—a name which suits their function, since they are usually filled with semen at the generation season. The seminal bladders communicate with the urinogenital cloaca by wide openings, and it is on the borders of these openings that the mouths of the Wolffian duct and ureters must be looked for. My embryological investigations, though they have not been specially directed to this point, seem to shew that the seminal bladders do not arise during embryonic life, and are still absent in very young individuals. It seems probable that both the bladders and the urinogenital cloaca are products of the lower extremities of the Wolffian duct. The only other duct requiring any notice in the male is the rudimentary oviduct. As was first shown by Semper, rudiments of the upper extremities of the oviducts, with their abdominal openings, are to be found in the male in the same position as in the female, on the front surface of the liver.

In the female the same ducts are present as in the male, viz. the Wolffian duct and the ureters. The part of the Wolffian duct which receives the secretion of the Wolffian body is not contorted, but is otherwise similar to the homologous part of the Wolffian duct in the male. The Wolffian ducts of the two sides fall independently into an unpaired urinal cloaca, but their lower ends, instead of remaining simple as in the male, become dilated into urinary bladders. *Vide* Pl. XIX. fig. 2. There were nine ureters in the example dissected, whose arrangement did not differ greatly from that in the male—the hinder ones remaining distinct from each other, but a certain amount of fusion, the extent of which could not be quite certainly ascertained, taking place between the anterior ones. The arrangement of the openings of these ducts is not quite the same as in the male. A somewhat magnified representation of it is given in Pl. XIX. fig. 3, *o. u.* The two Wolffian ducts meet at so acute an angle that their hindermost extremities are only separated by a septum. In the region of this septum on the inner walls of the two Wolffian ducts were situated the openings of the ureters, of which there were five on each side arranged linearly. In a second example, also adult, I found four distinct openings on each side similarly arranged to those in the specimen described. Professor Semper states that all the ureters in the female unite into a *single duct* before opening into the Wolffian duct. It will certainly surprise me to find such great variations in different individuals of this species as is implied by the discrepancy between Professor Semper's description and my own.

The main difference between the ureters in the male and female consists in their falling into the urinogenital cloaca in the former and into the Wolffian duct in the latter. Since, however, the urinogenital cloaca is a derivative of the Wolffian duct, this difference between the two sexes is not a very important one. The urinary cloaca opens, in the female, into the general cloaca by a median papilla of somewhat smaller dimensions than the corresponding papilla in the male. Seminal bladders are absent in the female, though possibly represented by the bladder-like dilatations of the Wolffian duct. The oviducts, whose anatomy is too well known to need description, open independently into the general cloaca.

Since the publication of Professor Semper's researches on the urinogenital system of Elasmobranch fishes, it has been well known that, in most adult Elasmobranchs, there are present a series of funnel-shaped openings, leading from the perivisceral cavity, by the intermediation of a short canal, into the glandular tubuli of the kidney. These openings are called by Professor Semper, *Segmentaltrichter*, and by Dr Spengel, in his valuable work on the urogenital system of Amphibia, *Nephrostomen.* In the present work the openings will be spoken of as segmental openings, and the tubes connected with them as segmental tubes. Of these openings there are a considerable number in the adults of both sexes of Scy. canicula, situated along the inner border of each kidney. The majority of them belong to the Wolffian body, though absent in the extreme anterior part of this. In very young examples a few certainly belong to the region of the kidney proper. Where present, there is one for each segment[1]. It is not easy to make certain of their exact number. In one male I counted thirteen. In the female it is more difficult than in the male to make this out with certainty, but in one young example, which had left the egg but a short time, there appeared to be at least fourteen present. According to Semper there are thirteen funnels in both sexes—a number which fairly well agrees with my own results. In the male, rudiments of segmental tubes are present in all the anterior segments of the Wolffian body behind the vasa efferentia, but it is not till about the tenth segment that the first complete one is present. In the female a somewhat smaller number of the anterior segments, six or seven, are without segmental tubes or only possess them in a rudimentary condition.

A typical segment of the Wolffian body or kidney, in the sense in which this term has been used above, consists of a number of factors each of which will be considered in detail with reference to its variations. On Pl. XIX. fig. 5, is represented

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[1] The term segment will be more accurately defined below.

a portion of the Wolffian body with three complete segments and part of a fourth. If one of these be selected, it will be seen to commence with (1) a segmental opening, somewhat oval in form (*st. o*) and leading directly into (2) a narrow tube, the segmental tube, which takes a more or less oblique course backwards, and, passing superficially to the Wolffian duct (*w. d*), opens into (3) a Malpighian body (*p. mg*) at the anterior extremity of an isolated coil of glandular tubuli. This coil forms the fourth section of each segment, and starts from the Malpighian body. It consists of a considerable number of rather definite convolutions, and after uniting with tubuli from one or two (according to size of the segment) accessory Malpighian bodies (*a. mg*), smaller than the one into which the segmental tube falls, eventually opens by a (5) narrowish tube into the Wolffian duct at the posterior end of the segment. Each segment is completely isolated (except for certain rudimentary structures to be alluded to shortly) from the adjoining ones, *and never has more than one segmental tube and one communication with the Wolffian duct.*

The number and general arrangement of the segmental tubes have already been spoken of. Their openings into the body cavity are, in Scyllium, very small, much more so than in the majority of Elasmobranchs. The general appearance of a segmental tube and its opening is somewhat that of a spoon, in which the handle represents the segmental tube, and the bowl the segmental opening. Usually amongst Elasmobranchs the openings and tubes are ciliated, but I have not determined whether this is the case in Scy. canicula, and Semper does not speak definitely on this point. From the segmental openings proceed the segmental tubes, which in the front segments have nearly a transverse direction, but in the posterior ones are directed more and more obliquely backwards. This statement applies to both sexes, but the obliquity is greater in the female than in the male.

As has been said, each segmental tube normally opens into a Malpighian body, from which again there proceeds the tubulus, the convolutions of which form the main mass of each segment. This feature can be easily seen in the case of the Malpighian bodies of the anterior part of the Wolffian gland in young examples, and sometimes fairly well in old ones, of either sex[1]. There is generally in each segment a second Malpighian body, which forms the commencement of a tubulus joining that from the primary Malpighian body, and, where the segments are larger, there are three, and possibly in the hinder segments of the Wolffian gland and segments of the kidney proper, more than three Malpighian bodies.

The accessory Malpighian bodies, or at any rate one of them, appear to have curious relations to the segmental tubes. The necks of some of the anterior segmental tubes (Pl. XIX. fig. 5) close to their openings into the primary Malpighian bodies are provided with a small knob of cells which points towards the preceding segment and is usually connected with it by a fibrous band. This knob is most conspicuous in the male, and in very young animals or almost ripe embryos. In several instances in a ripe male embryo it appeared to me to have a lumen, and to be continued directly forwards into the accessory Malpighian body of the preceding segment. One such case is figured in the middle segment on Pl. XIX. fig. 5. In this embryo segmental tubes were present in the segments immediately succeeding those connected with the vasa efferentia, and at the same time these segments contained ordinary and accessory Malpighian bodies. The segmental tubes of these segments were not, however, connected with the Malpighian body of their proper segment, but instead, turned forwards and entered the segment in front of that to which they properly belonged. I failed to trace them quite definitely to the accessory Malpighian body of the preceding segment, but, in one instance at least, there appeared to me to be present a fibrous connection, which is shewn in the figure already referred to, Pl. XIX. fig. 5, *r. st.* In any case it can hardly be doubted that this peculiarity of the foremost segmental tubes is related to what would seem to be the normal arrangement in the next few succeeding segments, where each segmental tube is connected with a Malpighian body in its own segment, and more or less distinctly with an accessory Malpighian body in the preceding segment.

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[1] My observations on this subject completely disprove, if it is necessary to do so after Professor Semper's investigations, the statement of Dr Meyer, that segmental tubes in Scyllium open into lymph organs.

In the male the anterior segmental tubes, which even in the embryo exhibit signs of atrophy, become in the adult completely aborted (as has been already shewn by Semper), and remain as irregular tubes closed at both ends, which for the most part do not extend beyond the Wolffian duct (Pl. XIX. fig. 4, *r. st*). In the adult, the first two or three segments with these aborted tubes contain only accessory Malpighian bodies; the remaining segments, with aborted segmental tubes, both secondary and primary Malpighian bodies. In neither case are the Malpighian bodies connected with the aborted tubes.

The Malpighian bodies in Scyllium present no special peculiarities. The outer layer of their capsule is for the most part formed of flattened cells; but, between the opening of the segmental tube and the efferent tubulus of the kidney, their cells become columnar. Vide Pl. XIX. fig. 5. The convoluted tubuli continuous with them are, I believe, ciliated in their proximal section, but I have not made careful investigations with reference to their finer structure. Each segment is connected with the Wolffian duct by a single tube at the hinder end of the segment. In the kidney proper, these tubes become greatly prolonged, and form the ureters.

It has already been stated that the semen is carried by vasa efferentia from the testes to the anterior segments of the Wolffian body, and thence through the coils of the Wolffian body to the Wolffian duct. The nature of the vasa will be discussed in the embryological section of this chapter: I shall here confine myself to a simple description of their anatomical relations. The consideration of their connections naturally falls under three heads: (1) the vasa efferentia passing from the testes to the Wolffian body, (2) the mode in which these are connected with the Wolffian body, and (3) with the testis.

In Pl. XIX. fig. 4, drawn for me from nature by my friend Mr Haddon, are shewn the vasa efferentia and their junctions both with the testes and the kidney. This figure illustrates better than any description the anatomy of the various parts. Behind there are two simple vasa efferentia (*v. e*) and in front a complicated network of vasa, which might be regarded as formed of either two or four main vessels. It will be shewn in the sequel that it is really formed of four distinct vessels.

Professor Semper states that there is but a single vas efferens in Scyllium canicula, a statement which appears to me unquestionably erroneous. All the vasa efferentia fall into a *longitudinal duct* (*l. c*), which is connected in succession with the several segments of the Wolffian body (one for each vas efferens) which appertain to the testis. The hind end of the longitudinal duct is simple, and ends blindly close to its junction with the last vas efferens; but in front, where the vasa efferentia are complicated, the longitudinal duct also has a complicated constitution, and forms a network rather than a simple tube. It typically sends off a duct to join the coils of the Wolffian body between each pair of vasa efferentia, and is usually swollen where this duct parts from it. A duct similar to this has been described by Semper as *Nierenrandcanal* in several Elasmobranchs, but its existence is expressly denied in the case of Scyllium! It is usually found in Amphibia, as we know from Bidder and Spengel's researches. Spengel calls it *Längscanal des Hoden;* the vessels from it into the kidney he calls *vasa efferentia,* and the vessels to it, which I speak of as vasa efferentia, he calls *Quercanale.*

The exact mode of junction of the separate vasa efferentia with the testis is difficult to make out on account of the opacity of the basal portion of the testis. My figure shews that there is a network of tubes (formed of four main tubes connected by transverse branches) which is a continuation of the anterior vasa efferentia, and joined by the two posterior ones. These tubes receive the tubuli coming from the testicular ampullæ. The whole network may be called, with Semper, the *testicular network.* While its general relations are represented in my figure, the opacity of the testes was too great to allow of all the details being with certainty filled in.

The kidneys of Scyllium stellare, as might be expected, closely resemble those of Scy. canicula. The ducts of the kidney proper, have, in the former species, a larger number of distinct openings into the urinogenital cloaca. In two male examples I counted seven distinct ureters, though it is not impossible that there may have been one or two more present. In one of my examples the ureters had seven distinct openings into the cloaca, in the other five openings. In a female I counted eleven ureters opening into the Wolffian duct by seven distinct openings. In the remaining parts of the excretory organs the two species of Scyllium resemble each other very closely.

As may be gathered from Prof. Semper's monograph, the excretory organs of Scyllium canicula are fairly typical for Elasmobranchs generally. The division into kidney and Wolffian body is universal. The segmental openings may be more numerous and larger, *e.g.* Acanthias and Squatina, or absent in the adult, *e.g.* Mustelus and Raja. Bladder-like swellings of the Wolffian duct in the female appear to be exceptional, and seminal bladders are not always present. The variations in the ureters and their openings are considerable, and in some cases all the ureters are stated to fall into a single duct, which may be spoken of as the ureter par excellence[1], with the same relations to the kidneys as the Wolffian duct bears to the Wolffian body. In some cases Malpighian corpuscles are completely absent in the Wolffian body, *e.g.* Raja.

The vasa efferentia of the testes in Scyllium are very typical, but there are some forms in which they are more numerous as well as others in which they are less so. Perhaps the vasa efferentia are seen in their most typical form in Centrina as described and figured (Pl. XXI.) by Professor Semper, or in Squatina vulgaris, as I find it, and have represented it on Pl. XIX. fig. 8. From my figure, representing the anterior part of the Wolffian body of a nearly ripe embryo, it will be seen that there are five vasa efferentia (*v. e*) connected on the one hand with a longitudinal canal at the base of the testes (*n. t*) and on the other with a longitudinal canal in the Wolffian body. Connected with the second longitudinal canal are four Malpighian bodies, three of them stalked and one sessile; from which again proceed tubes forming the commencements of the coils of the anterior segments of the Wolffian body. These Malpighian bodies are clearly my primary Malpighian bodies, but there are in Squatina, even in the generative segments, secondary Malpighian bodies. What Semper has described

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[1] I feel considerable hesitation in accepting Semper's descriptions of the ureters and their openings. It has been shewn above that for Scyllium his statements are probably inaccurate, and in other instances, *e.g.* Raja, I cannot bring my dissections to harmonise with his descriptions.

for Centrina and one or two other genera, closely correspond with what is present in Squatina.

Development of the Segmental Tubes.

On p. 127, *et seq.* an account was given of the first formation of the segmental tubes and the segmental duct, and the history of these bodies was carried on till nearly the period at which it is taken up in the exhaustive Memoir of Professor Semper. Though the succeeding narration traverses to a great extent the same ground as Semper's Memoir, yet many points are treated somewhat differently, and others are dealt with which do not find a place in the latter. In the majority of instances, attention is called to points on which my results either agree with, or are opposed to, those of Professor Semper.

From previous statements it has been rendered clear that *at first* the excretory organs of Elasmobranchs exhibit no division into Wolffian body or kidney proper. Since this distinction is merely a question of the ducts, and does not concern the glandular tubuli, no allusion is made to its appearance in the present section, which deals only with the glandular part of the kidneys and not with their ducts.

Up to the close of stage K the urinogenital organs consist of a segmental duct opening in front into the body cavity, and terminating blindly behind in close contact with the cloaca, and of a series of segmental tubes, each opening into the body cavity on the inner side of the segmental duct, but ending blindly at their opposite extremities. It is with these latter that we have at present to deal. They are from the first directed obliquely backwards, and coil close round the inner and dorsal sides of the segmental duct. Where they are in contact (close to their openings into the body cavity) with the segmental duct, the lumen of the latter diminishes and so comes to exhibit regular alternations of size. This is shewn in Pl. XI. fig. 18 *s. d.* At the points where the segmental duct has a larger lumen, it eventually unites with the segmental tubes.

The segmental tubes rapidly undergo a series of changes, the character of which may be investigated, either by piecing together transverse sections, or more easily from longitudinal and vertical sections. They acquire a Λ-shaped form with an anterior limb opening into the body cavity and posterior limb, resting on a dilated portion of the segmental duct. The next important change which they undergo consists in a junction being effected between their posterior limbs, and the segmental duct. In the anterior part of the body these junctions appear before the commencement of stage L. A segmental tube at this stage is shewn in longitudinal section on Pl. XX. fig. 7*a*, and in transverse section on Pl. XVII. fig. 2. In the former the actual openings into the body cavity are not visible. In the transverse section only one limb of the Λ is met with on either side of the section; the limb opening into the body cavity is seen on the left side, and that opening into the segmental duct on the right side. This becomes quite intelligible from a comparison with the longitudinal section which demonstrates that it is clearly not possible to see more than a single limb of the Λ in any transverse section.

After the formation of their junctions with the segmental duct, other changes soon take place in the segmental tubes. By the close of stage L four distinct divisions may be noticed in each tube. Firstly, there is the opening into the body cavity, with a somewhat narrow stalk, to which the name segmental tube will be strictly confined in the future, while the whole products of the original segmental tube will be spoken of as a segment of the kidney. This narrow stalk opens into a vesicle (Pl. XVII. fig. 2, and XX. fig. 6), which forms the second division. From the vesicle proceeds a narrower section forming the third division, which during stage L remains very short, though in later stages it grows with great rapidity. It leads into the fourth division, which constitutes the posterior limb of the Λ, and has the form of a dilated tube with a narrow opening into the segmental duct.

The subsequent changes of each segment do not for the most part call for much attention. They consist mainly in the elongation of the third division, and its conversion into a coiled tubulus which then constitutes the main mass of each segment of the kidney. There are, however, two points of some interest, viz.: (1) the formation of the Malpighian bodies, and (2) the establishment of the connection between each segmental tube and the tubulus of the preceding segment which was alluded to in the description on p. 256. The development of the Malpighian body is intimately linked with that of the secondary connection between two segments. They are both products of the metamorphosis of the vesicle which forms the termination of the segmental tube proper.

At about stage O this vesicle grows out in two directions (Pl. XX. fig. 10), viz. towards the segment in front (*p.x*) and posteriorly into the segment of which it properly forms a part (*mg*). That portion which grows backward remains continuous with the third division of its proper segment, and becomes converted into a Malpighian body. It assumes (Pl. XX. figs. 6 and 10) a hemispherical form while near one edge of it is the opening from a segmental tube, and near the other the opening leading into a tubulus of the kidney. The two-walled hemisphere soon grows into a nearly closed sphere, with a central cavity into which projects a vascular tuft. For this tuft the thickened inner wall of cells forms a lining, and at the same time the outer wall becomes thinner, and formed of flattened cells, except in the interval between the openings of the segmental tube and kidney tubulus, where its cells remain columnar.

The above account of the formation of the Malpighian bodies agrees very well with the description which Pye[1] has given of the formation of these bodies in the embryonic Mammalian kidney. My statements also agree with those of Semper, in attributing the formation of the Malpighian body to a metamorphosis of part of the vesicle at the end of the segmental tube. Semper does not however enter into full details on this subject.

The elucidation of the history of the second outgrowth from the original vesicle towards the preceding segment is fraught with considerable difficulties, which might no doubt be overcome by a patient investigation of ample material, but which I have not succeeded in fully accomplishing.

The points which I believe myself to have determined are illustrated by fig. 10, Pl. XX., a longitudinal vertical section through a portion of the kidney between stages O and P. In this figure parts of three segments of the kidney are represented. In the hindermost of the three—the one to the right—there is a complete segmental tube (*s.t*) which opens at its upper

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[1] *Journal of Anatomy and Physiology*, Vol. IX.

extremity into an irregular vesicle, prolonged *behind* into a body which is obviously a developing Malpighian body, *m. g*, and in *front* into a wide tube cut obliquely in the section and ending apparently blindly (*p. x*). In the preceding segment there is also a segmental tube (*s. t*) whose opening into the body cavity passes out of the plane of the section, but which is again connected with a vesicle dilating behind into a Malpighian body (*m. g*) and in front into the irregular tube (*p. x*) as in the succeeding segment, *but this tube is now connected* (and this could be still more completely seen in the segment in front of this) *with a vesicle which opens into the thick-walled collecting tube* (*fourth division*) *of the preceding segment* close to the opening of the latter into the Wolffian duct. The fact that the anterior prolongation of the vesicle ends blindly in the hindermost segment is due of course to its terminal part passing out of the plane of the section. *Thus we have established between stages O and P a connection between each segmental tube and the collecting tube of the segment in front of that to which it properly belongs; and it further appears that in consequence of this each segment of the kidney contains two distinct coils of tubuli which only unite close to their common opening into the Wolffian duct!*

This remarkable connection is not without morphological interest, but I am unfortunately only able to give in a fragmentary manner its further history. During the greater part of embryonic life a large amount of interstitial tissue is present in the embryonic kidneys, and renders them too opaque to be advantageously studied as a whole; and I have also, so far, failed to prepare longitudinal sections suitable for the study of this connection. It thus results that the next stage I have satisfactorily investigated is that of a nearly ripe embryo already spoken of in connection with the adult, and represented on Pl. XIX. fig. 5. This figure shews that each segmental tube, while distinctly connected with the Malpighian body of its own segment, also sends out a branch towards the secondary Malpighian body of the preceding segment. This branch in most cases appeared to be rudimentary, and in the adult is certainly not represented by more than a fibrous band, but I fancy that I have been able to trace it (though not with the distinctness I could desire) in surface views of the embryonic kidney of stage Q. *The condition of the Wolffian body represented on Pl.* XIX. *fig.* 5 *renders it probable that the accessory Malpighian body in each segment is developed in connection with the anterior growth from the original vesicle at the end of the segmental tube of the succeeding segment.* How the third or fourth accessory Malpighian bodies, when present, take their origin I have not made out. It is, however, fairly certain that they form the commencement of two additional coils which unite, like the coil connected with the first accessory Malpighian body, with the collecting tube of the primitive coil close to its opening into the Wolffian duct or ureter.

The connection above described between two successive kidney segments appears to have escaped Professor Semper's notice, though I fancy that the peculiar vesicle he describes, *loc. cit.* p. 303, as connected with the end of each segmental tube, is in some way related to it. It seems possible that the secondary connection between the segmental tube and the preceding segment may explain a peculiar observation of Dr Spengel[1] on the kidney of the tailless Amphibians. He finds that, in this group, the segmental tubes do not open into Malpighian bodies, but into the fourth division of the kidney tube. Is it not just possible that in this case the primitive attachment of the segmental tubes may have become lost, and a secondary attachment, equivalent to that above described, though without the development of a secondary Malpighian body, have been developed? In my embryos the secondary coil of the segmental tubes opens, as in the Anura, into the fourth section of a kidney tubulus.

Development of the Müllerian and Wolffian ducts.

The formation of the Müllerian and Wolffian ducts out of the original segmental duct has been dealt with in a masterly manner by Professor Semper, but though I give my entire assent to his general conclusions, yet there are a few points on which I differ from him. These are for the most part of a

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[1] *Loc. cit.* pp. 85—89.

secondary importance; but they have a certain bearing on the homology between the Müllerian duct of higher Vertebrates and that of Elasmobranchs. The following account refers to Scy. canicula, but so far as my observations go, the changes in Scy. stellare are nearly identical in character.

I propose treating the development of these ducts in the two sexes separately, and begin with the female.

Shortly before stage N a horizontal split arises in the segmental duct[1], commencing some little distance from its anterior extremity, and extending backwards. This split divides the duct into a dorsal section and a ventral one. The dorsal section forms the Wolffian duct, and receives the openings of the segmental tubes, and the ventral one forms the Müllerian duct or oviduct, and is continuous with the unsplit anterior part of the primitive segmental duct, which opens into the body-cavity. The nature of the splitting may be gathered from the woodcut, fig. 6, p. 281, where x represents the line along which the segmental duct is divided. The splitting of the primitive duct extends slowly backwards, and thus there is for a considerable period a single duct behind, which bifurcates in front. A series of transverse sections through the point of bifurcation always exhibits the following features. Anteriorly two separate ducts are present, next two ducts in close juxtaposition, and immediately behind this a single duct. A series of sections through the junction of two ducts is represented on Plate XX. fig. 1 *A*, 1 *B*, 1 *C*, 1 *D*.

In my youngest example, in which the splitting had commenced, there were two separate ducts for only 14 sections, and in a slightly older one for about 18. In the second of these embryos the part of the segmental duct anterior to the front end of the Wolffian duct, which is converted directly into the oviduct, extended through 48 sections. In the space included in these 48 sections at least five, and I believe six, segmental tubes with openings into the body-cavity were present. These segmental tubes did not however unite with the oviduct, or at best, but one or two rudimentary junctions were visible, and the evidence of my earlier embryos appears to shew that the segmental tubes in front of the Wolffian duct never become in

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[1] For the development of the segmental duct, *vide* p. 127, *et seq.*

the female united with the segmental duct. The anterior end of the Wolffian duct is very much smaller than the oviduct adjoining it, and as the reverse holds good in the male, an easy method is afforded of distinguishing the two sexes even at the earliest period of the formation of the Wolffian duct.

Hitherto merely the general features of the development of the oviduct and Wolffian duct have been alluded to, but a careful inspection of any good series of sections, shewing the junction of these two ducts, brings to light some features worth noticing in the formation of the oviduct. It might have been anticipated that, where the two ducts unite behind as the segmental duct, their lumens would have nearly the same diameter, but normally this appears to be far from the case.

To illustrate the formation of the oviduct I have represented a series of sections through a junction in an embryo in which the splitting into two ducts had only just commenced (Pl. XX. fig. 1), but I have found that the features of this series of sections are exactly reproduced in other series in which the splitting has extended as far back as the end of the small intestine. In the series represented (Pl. XX.) 1 A is the foremost section, and 1 D the hindermost. In 1 A the oviduct (*o d*) is as large or slightly larger than the Wolffian duct (*w.d*), and in the section in front of this (which I have not represented) was considerably the larger of the two ducts. In 1 B the oviduct has become markedly smaller, but there is no indication of its lumen becoming united with that of the Wolffian duct—the two ducts, though in contact, are distinctly separate. In 1 C the walls of the two ducts have fused, and the oviduct appears merely as a ridge on the under surface of the Wolffian duct, and its lumen, though extremely minute, *shews no sign of becoming one with that of the Wolffian duct.* Finally, in 1 D the oviduct can merely be recognised as a thickening on the under side of the segmental duct, as we must now call the single duct, but a slight bulging downwards of the lumen of the segmental duct appears to indicate that the lumens of the two ducts may perhaps have actually united. But of this I could not be by any means certain, and it seems quite possible that the lumen of the oviduct never does open into that of the segmental duct.

The above series of sections goes far to prove that the posterior part of the oviduct is developed as a nearly solid ridge split off from the under side of the segmental duct, into which at the utmost a very small portion of the lumen of the latter is continued. One instance has however occurred amongst my sections which probably indicates that the lumen of the segmental duct may sometimes, in the course of the formation of the oviduct and Wolffian duct, become divided into two parts, of which that for the oviduct, though considerably smaller than that for the Wolffian duct, is not so markedly so as in normal cases (Pl. XX. fig. 2).

Professor Semper states that the lumen of the part of the oviduct split off from the hindermost end of the segmental duct becomes continuously smaller, till at last close to the cloaca it is split off as a solid rod of cells without a lumen, and thus it comes about that the oviduct, when formed, ends blindly, and does not open into the cloaca till the period of sexual maturity. My own sections do not include a series shewing the formation of a terminal part of the oviduct, but Semper's statements accord precisely with what might probably take place if my account of the earlier stages in the development of the oviduct is correct. The presence of a hymen in young female Elasmobranchs was first made known by ~~Putmann and~~ Garman[1], and subsequently discovered independently by Semper[2].

The Wolffian duct appears to receive its first segmental tube at its anterior extremity.

In the male the changes of the original segmental duct have a somewhat different character to those in the female, although there is a fundamental agreement between the two sexes. As in the female a horizontal split makes its appearance a short way behind the front end of the segmental duct, and divides this into a dorsal Wolffian duct and a ventral Müllerian duct, the latter continuous with the anterior section of the segmental duct, which carries the abdominal opening. The differences in development between the two sexes are, in spite of a general similarity, very obvious. In the first place, the

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[1] On the Male and Female Organs of Sharks and Skates, with special reference to the use of the claspers, *Proceed. American Association for Advancement of Science*, 1874.

[2] *Loc. cit.*

ventral portion split off from the segmental duct, instead of being as in the female larger in front than the Wolffian duct, is very much smaller; while behind it does not form a continuous duct, but in some parts a lumen is present, and in others again absent (Pl. XX. fig. 6). It does not even form an unbroken cord, but is divided in disconnected portions. Those parts with a lumen do not appear to open into the Wolffian duct.

The process of splitting extends gradually backwards, so that there is a much longer rudimentary Müllerian duct by stage O than by stage N. By stage P the posterior portions of the Müllerian ducts have vanished. The anterior parts remain, as has been already stated, till adult life. A second difference between the male and female depends on the fact that, in the male, the splitting of the segmental duct into Müllerian duct and Wolffian duct never extends beyond the hinder extremity of the small intestine. A third and rather important point of difference consists in the splitting commencing far nearer the front end of the segmental duct in the male than in the female. In the female it was shewn that about 48 sections intervened between the front end of the segmental duct and the point where this became split, and that this region included five or six segmental tubes. In the male the homologous space only occupies *about* 7 *to* 12 *sections, and does not contain the rudiment of more than a single segmental tube.* Although my sections have not an absolutely uniform thickness, yet the above figures suffice to shew in a conclusive manner that the splitting of the segmental duct commences far further forwards in the male than in the female. This difference accounts for two facts which were mentioned in connection with the excretory organs of the adult, viz. (1) the greater length of the Wolffian body in the male than in the female, and (2) the fact that although a nearly similar number of segmental tubes persist in the adults of both sexes, yet that in the male there are five or six more segments in front of the first fully developed segmental opening than in the female.

The above description of the formation of the Müllerian duct in the male agrees very closely with that of Professor Semper for Acanthias. For Scyllium however he denies, as it appears to me erroneously, the existence of the posterior rudimentary parts of the Müllerian duct. He further asserts that the portions of the Müllerian duct with a lumen open into the Wolffian duct. The most important difference, however, between Professor Semper's and my own description consists in his having failed to note that the splitting of the segmental duct commences much further forwards in the male than in the female.

I have attempted to shew that the oviduct in the female, with the exception of the front extremity, is formed as a nearly solid cord split off from the ventral surface of the segmental duct, and not by a simple splitting of the segmental duct into two equal parts. If I am right on this point, it appears to me far easier to understand the relationship between the oviduct or Müllerian duct of Elasmobranchs and the Müllerian duct of Birds, than if Professor Semper's account of the development of the oviduct is the correct one. Both Professor Semper and myself have stated our belief in the homology of the ducts in the two cases, but we have treated their relationship in a very different way. Professor Semper[1] finds himself compelled to reject, on theoretical grounds, the testimony of recent observers on the development of the Müllerian duct in Birds, and to assert that it is formed out of the Wolffian duct, or, according to my nomenclature, 'the segmental duct.' In my account[2], the ordinary statements with reference to the development of the Müllerian duct in Birds are accepted; but it is suggested that the independent development of the Müllerian duct may be explained by the function of this duct in the adult having, as it were, more and more impressed itself upon the embryonic development, till finally all connection, even during embryonic life, between the oviduct and the segmental duct (Wolffian duct) became lost.

Since finding what a small portion of the segmental duct became converted into the Müllerian duct in Elasmobranchs, I have reexamined the development of the Müllerian duct in the Fowl, in the hope of finding that its posterior part might develope nearly in the same manner as in Elasmobranchs, at the expense of a thickening of cells on the outer surface of

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[1] *Loc. cit.* p. 412, 413.

[2] The Urinogenital Organs of Vertebrates, *Journal of Anatomy and Physiology*, Vol. x. p. 47.

the Wolffian duct. I have satisfied myself, in conjunction with Mr Sedgwick, that this is not the case, and that the general account is in the main true; but at the same time we have obtained evidence which tends to shew that the cells which form the Müllerian duct are in part derived from the walls of the Wolffian duct. We propose giving a full account of our observations on this point, so that I refrain from mentioning further details here. It may however be well to point out that, apart from observations on the actual development of the Müllerian duct in the Bird, the fact of its abdominal opening being situated some way behind the front end of the Wolffian duct, is of itself a sufficient proof that it cannot be the metamorphosed front extremity of the Wolffian (= segmental) duct, in the same way that the abdominal opening of the Müllerian duct is the front extremity of the segmental duct in Elasmobranchs.

Although the evidence I can produce in the case of the Fowl of a direct participation of the Wolffian duct in the formation of the Müllerian is not of an absolutely conclusive kind, yet I am inclined to think that the complete independence of the two ducts, if eventually established as a fact, would not of itself be sufficient (as Semper is inclined to think) to disprove the identity of the Müllerian duct in Birds and Elasmobranchs.

We have, no doubt, almost no knowledge of the magnitude of the changes which can take place in the mode of development of the same organ in different types, yet this would have to be placed at a very low figure indeed in order to exclude the possibility of a change from the mode of development of the Müllerian duct in Elasmobranchs to that in Birds. We have, it appears to me, in the smallness of the portion of the segmental duct which goes to form the Müllerian duct in Elasmobranchs, evidence that a change has already appeared in this group in the direction of a development of the Müllerian duct independent of the segmental duct, and therefore of the Wolffian duct; and it has been in view of this consideration, that I have devoted so much attention to the apparently unimportant point of how much of the segmental duct was concerned in the formation of the Müllerian duct. An analogous change, in a somewhat different direction, would seem to be taking place in the development of the rudimentary Müllerian duct in the male Elasmobranchs.

It is, perhaps, just worth pointing out, that the blindness of the oviduct of female Elasmobranchs, and its mode of development from an imperfect splitting of the segmental duct, may probably be brought into connection with the blindness of the extremity of the Müllerian duct or oviduct which so often occurs in both sexes of Sturgeons (Accipenser).

I may, perhaps, at this point, be permitted to say a few words about my original account of the development of the Wolffian duct. This account was incorrect, and based upon a false interpretation of an imperfect series of sections, and I took the opportunity, in a general account of the urinogenital system of Vertebrates, to point out my mistake[1]. Professor Semper has, however, subsequently done me the honour to discuss, at considerable length, my original errors, and to attempt to explain them. Since it appears to me improbable that the continuation of such a discussion can be of much general interest, it will suffice to say now, that both Professor Semper's and my own original statements on the development of the Wolffian duct were erroneous; but that both of us have now recognised our mistakes; and that the first morphologically correct account of the development was given by him.

With reference to the formation of the urinal cloaca there is not much to say. The originally widely separated openings of the two Wolffian ducts gradually approximate in both sexes. By stage O (Pl. XVIII. fig. 1 *b*) they are in close contact, and the lower ends of the two ducts actually coalesce at a somewhat later period, and open by a single aperture into the common cloaca. The papilla on which this is situated begins to make its appearance considerably before the actual fusion of the lower extremities of the two ducts.

Formation of Wolffian Body and Kidney proper.

Between stages L and M the hindermost ten or eleven segments of the primitive undivided excretory organ commence to undergo changes which result in their separation from the

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[1] *Journal of Anatomy and Physiology*, Vol. x. 1875.

anterior segments as a distinct gland, which was spoken of in the description of the adult as the kidney proper, while the unaltered preceding segments of the kidney were spoken of as the Wolffian body.

It will be remembered that each segment of the embryonic kidney consists of four divisions, the last or fourth of which opens into the Wolffian duct. The changes which take place in the hindermost ten or eleven segments, and cause them to become distinguished as the kidney proper, concern alone the fourth division of each segment, which becomes prolonged backwards, and its opening into the Wolffian duct proportionately shifted. These changes affect the foremost segments of the kidney much more than the hindermost, so that the fourth division in the foremost segments becomes very much longer than in the hindermost, and at last all the prolongations of the kidney segments come to open nearly on the same level, close to the cloacal termination of the Wolffian duct (Pl. xx. fig. 8). The prolongations of the fourth division of the kidney-segments have already (p. 251) been spoken of in the description of the adult as ureters, and this name will be employed for them in the present section.

The exact manner in which the changes, that have been briefly related, take place is rather curious, and very difficult to unravel without the aid of longitudinal sections. First of all, the junction between each segment of the kidney and the Wolffian duct becomes so elongated as to occupy the whole interval between the junctions of the two neighbouring segments. The original opening of each tube into the Wolffian duct is situated at the anterior end of this elongated attachment, the remaining part of the attachment being formed solely of a ridge of cells on the dorsal side of the Wolffian duct. The general character of this growth will be understood by comparing fig. 7 *a* and 7 *b*, Pl. xx.—two longitudinal vertical sections through part of the kidneys. Fig. 7 *a* shews the normal junction of a segmental tube with the Wolffian duct in the Wolffian body, while in figure 7 *b* (*r. u*) is shewn the modified junction in the region of the kidney proper in the same embryo. The latter of these figures (fig. 7 *b*) appears to me to prove that the elongation of the attachments between the segmental tubes and Wolffian duct takes place *entirely at the expense of the former*. Owing to the length of this attachment, every transverse section through the kidney proper at this stage either presents a solid ridge of cells closely adhering to the dorsal side of the Wolffian duct, or else passes through one of the openings into the Wolffian duct.

During stage M the original openings of the segmental tubes into the Wolffian duct appear to me to become obliterated, and at the same time the lumen of each ureter is prolonged into the ridge of cells on the dorsal wall of the duct.

Both of these changes are illustrated in my figures. The fact of the obliteration of the original opening into the Wolffian duct is shewn in longitudinal section in Pl. XX. fig. 9, *u*, but more conclusively in the series of transverse sections represented on Pl. XX. fig. 3 A, 3 B, 3 C. In the hindermost of these (3 C) is seen the solid terminal point of a ureter, while the same ureter possesses a lumen in the two previous sections, but exhibits no signs of opening into the Wolffian duct. Sections may however be met with which appear to shew that in some instances the ureters still continue to open into the Wolffian duct, but these I find to be rare and inconclusive, and am inclined to regard them as abnormalities. The prolongation of the lumen of the ureters takes place in a somewhat peculiar fashion. The lumen is not, as might be expected, *completely* circumscribed by the wall of the ureter, but only *dorsally and to the sides*. Ventrally it is closed in by the dorsal wall of the Wolffian duct. In other words, each ureter is at first an incomplete tube. This peculiarity is clearly shewn in the middle figure of the series on Pl. XX. fig. 3 B.

During stages M and N the ureters elongate considerably, and, since the foremost ones grow the most rapidly, they soon come to overlap those behind. As each ureter grows in length it remains an incomplete tube, and its lumen, though proportionately prolonged, continues to present the same general relations as at first. It is circumscribed by its proper walls only dorsally and laterally; its floor being formed in the case of the front ureter by the Wolffian duct, and in the case of each succeeding ureter by the dorsal wall of the ureter in front. This is most easily seen in longitudinal sections, and is represented on Pl. xx. fig. 9, or on a larger scale in fig. 9 A. In the latter figure it is especially clear that while the wall on the dorsal side of the lumen of each ureter is continuous with the dorsal wall of the tubulus of its own segment, the wall on the ventral side is continuous with the dorsal wall of the ureter of the preceding segment. This feature in the ureters explains the appearance of transverse sections in which the ureters are not separate from each other, but form together a kind of ridge on the dorsal side of the Wolffian duct, in which there are a series of perforations representing the separate lumens of the ureters (Pl. xx. fig. 4). The peculiarities in the appearance of the dorsal wall of the Wolffian duct in fig. 9 A, and the difference between the cells composing it and those of the ventral wall, become intelligible on comparing this figure with the representation of transverse section in fig. 3 B and 3 C, and especially in fig. 4. Most of the ureters continue to end blindly at the close of stage N, and appear to have solid posterior terminations like that of the Müllerian duct in Birds.

By stage O all the ureters have become prolonged up to the cloacal end of the Wolffian duct, so that the anterior one has a length equal to that of the whole kidney proper. For the most part they acquire independent openings into the end section of the Wolffian duct, though some of them unite together before reaching this. The general appearance of the hindermost of them between stages N and O is shewn in longitudinal and vertical section in Pl. xx. fig. 8, *u*.

They next commence to develope into complete and independent tubes by their side walls growing inwards and meeting below so as to completely enclose their lumen. This is seen already to have occurred in most of the posterior ureters in Pl. xx. fig. 8.

Before stage P the ureters cease to be united into a continuous ridge, and each becomes separated from its neighbours by a layer of indifferent tissue: by this stage, in fact, the ureters have practically attained very nearly their adult condition. The general features of a typical section through them are shewn on Pl. xx. fig. 5. The figure represents the section of a female embryo, not far from the cloaca. Below is the oviduct (*o d*). Above this again is the Wolffian duct (*w.d*), and still dorsal to this are four ureters (*u*). In female embryos more than four ureters are not usually to be seen in a single section. This is probably owing to the persistence, in some instances, of the intimate connection between the ureters found at an earlier stage of development, and results in a single ureter coming to serve as the collecting duct for several segments. A section through a male embryo of stage P would mainly differ from that through a female in the absence of the oviduct, and in the presence of probably six[1], instead of four, ureters.

The exact amount of fusion which takes place between the ureters, and the exact number of the ureters, cannot easily be determined from sections, but the study of sections is chiefly of value in shewing the general nature of the changes which take place in the process of attaining the adult condition.

It may be noticed, as a consequence of the above account, that the formation of the ureters takes place by a growth of the original segmental tubes, and not by a splitting off of parts of the wall of the Wolffian duct.

The formation of ureters in Scyllium, which has been only very cursorily alluded to by Professor Semper, appears to differ very considerably from that in Acanthias as narrated by him.

The Vasa Efferentia.

A comparison of the results of Professor Semper on Elasmobranchs, and Dr Spengel on Amphibians, suggests several interesting questions with reference to the development of the vasa efferentia, and the longitudinal canal of the Wolffian body.

Professor Semper was the first to describe the adult anatomy and development of vasa efferentia in Elasmobranchs, and the following extracts will fully illustrate his views with reference to them.

"In[2] dem frühesten Stadium finden sich wie früher angegeben ungefähr 34 Trichter in der Liebeshöhle, von diesen gehen die 27 hintersten in die persistirenden Segmentaltrichter

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[1] This at least holds good for one of my embryos at this stage, which is labelled Scy. canicula, but which may possibly be Scy. stellare.

[2] *Loc. cit.* p. 364.

über, von denen 4 beim erwachsenen Thiere auf dem Mesorchium stehen. Die übrigen 7 schliessen sich vollständig ab zu den erwähnten länglichen und später mannigfach auswachsenden varicösen Trichterblasen; von diesen sind es wiederum 3—4 welche untereinander in der Längsrichtung verwachsen und dadurch den in der Basis der Hodenfalte verlaufenden Centralcanal des Hodens bilden. Ehe aber diese Verwachsung zu einem mehr oder minder geschlängelten Centralcanal vollständig wird, hat sich einmal das Lumen der Trichterblasen fast vollständig geschlossen und ausserdem von ihnen aus durch Verwachsung und Knospung die erste Anlage des rete vasculosum Halleri gebildet (Taf. XX. Fig. 1, 2 *c*). Es erstreckt sich nämlich mehr oder minder weit in die Genitalfalte hinein ein unregelmässiges von kleinen Zellen begränztes Canalnetz welches zweifellos mit dem noch nicht ganz vollständigen Centralcanale des Hodens (Taf. XX. fig. 2 *c*) in Verbindung steht. Von diesem letzteren aus gehen in regelmässigen Abständen die Segmentalgänge (Taf. XX. fig. 2 *sg.*) gegen die Niere hin; da sie meist stark geneigt oder selbst geschlängelt (bei $6^{ctm.}$ langen Embryonen) gegen die Niere zu verlaufen, wo sie sich an die primären *Malpighi*'schen Körperchen und deren Bildungsblasen ansetzen, so kann ein verticaler Querschnitt auch nie einen solchen nun zum vas efferens gewordenen Segmentalgang seiner ganzen Länge nach treffen. Gegen die Trichterfurche zu aber steht namentlich am hinteren Theile der Genitalfalte der Centralcanal häufig noch durch einen kurzen Zellstrang mit dem Keimepithel der Trichterfurche in Verbindung; mitunter findet sich hier sogar noch eine kleine Höhlung, Rest des ursprünglich hier vorhandenen weiten Trichters" (Taf. XX. Fig. 3 *c*).

And again: "Dieser[1] Gegensatz in der Umbildung der Segmentalgänge an der Hodenbasis scheint nun mit einem anderen Hand in Hand zu gehen. Es bildet sich nämlich am Innenrande der Niere durch Sprossung und Verwachsung der Segmentalgänge vor ihrer Insertion an das primäre *Malpighi*'sche Körperchen ein Canal beim Männchen aus, den ich als *Nierenrandcanal* oben bezeichnet habe. Ich habe denselben bei Acanthias Centrina (Taf. XXI. Fig. 13) und Mustelus (Taf. XV. Fig. 8) gefunden.

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[1] *Loc. cit.* p. 395.

Bei Centrina ist er ziemlich lang und vereinigt mindestens 7 Segmentalgänge, aber von diesen letzteren stehen nur 5 mit dem Hodennetz in Verbindung. Dort nun wo diese letzteren sich an den Nierenrandcanal ansetzen (Taf. XXI. Fig. 13 sg.$_1$—sg.$_5$) findet sich jedesmal ein typisch ausgebildetes *Malpighi*'sches Körperchen mit dem aber nun nicht mehr wie ursprünglich nur 2 Canäle verbunden sind (Taf. XXI. Fig. 14) sondern 3. Einer dieser letzteren ist derjenige Ast des Nierenrandcanals welcher die Verbindung mit dem nächst folgenden Segmentalgang zu besorgen hat. An den Stellen aber wo sich an den Nierenrandcanal die hinteren blind gegen den Hoden hin endenden Segmentalgänge ansetzen fehlen diese *Malpighi*'schen Körperchen (Taf. XXI. fig. 13 *sg*$_7$) vollständig. Auch bei Mustelus (Taf. XV. Fig. 8, 10) findet genau dasselbe Verhältniss statt; da aber hier nur 2 (oder 3) Segmentalgänge zu vasa efferentia umgewandelt werden, so stehen hier am kurzen Randcanal der Niere auch nur 2 oder 3 *Malpighi*'sche Körperchen. Diese aber sind typisch ausgebildet (Taf. XV. Fig. 10)."

From these two extracts it is clear that Semper regards both the vasa efferentia, and central canal of the testis network, as well as the longitudinal canal of the Wolffian body, as products of the anterior segmental tubes.

The appearance of these various parts in the fully grown embryos or adults of such genera as Acanthias and Squatina strongly favours this view, but Semper appears to have worked out the development of these structures somewhat partially and by means of sections, a method not, in Scyllium at least, very suitable for this particular investigation. I myself at first unhesitatingly accepted Semper's views, and it was not till after the study of the paper of Dr Spengel on the Amphibian kidney that I came to have my doubts as to their accuracy. The arrangement of the parts in most Amphibians is strikingly similar to that in Elasmobranchs. From the testis come transverse canals corresponding with my vasa efferentia; these fall into a longitudinal canal of the kidneys, from which again, as in Squatina (Pl. XIX. fig. 8), Mustelus and Centrina, canals (the vasa efferentia of Spengel) pass off to Malpighian bodies. So far there is no difficulty, but Dr Spengel has made the extremely important discovery, that in young Amphibians each Malpighian body in the region of the generative ducts, in addition to receiving the vasa efferentia, is connected with a fully developed segmental tube opening into the body-cavity. In Amphibians, therefore, it is improbable that the vasa efferentia are products of the open extremities of the segmental tubes, considering that these latter are found in their unaltered condition at the same time as the vasa efferentia. When it is borne in mind how strikingly similar in most respects is the arrangement of the testicular ducts in Amphibia and Elasmobranchs, it will not easily be credited that they develope in entirely different methods. Since then we find in Amphibians fully developed segmental tubes in the same segments as the vasa efferentia, it is difficult to believe that in Elasmobranchs the same vasa efferentia have been developed out of the segmental tubes by the obliteration of their openings.

I set myself to the solution of the origin of the vasa efferentia by means of surface views, after the parts had been made transparent in creosote, but I have met with great difficulties, and so far my researches have only been partially successful. From what I have been able to see of Squatina and Acanthias, I am inclined to think that the embryos of either of these genera would form far more suitable objects for this research than Scyllium. I have had a few embryos of Squatina which were unfortunately too old for my purpose.

Very early the vasa efferentia are fully formed, and their arrangement in an embryo eight centimetres long is shewn in Pl. XIX. fig. 6, *v.e.* It is there seen that there are six if not seven vasa efferentia connected with a longitudinal canal along the base of the testes (Semper's central canal of the testis), and passing down like the segmental tubes to spaces between the successive segments of the Wolffian body. They were probably connected by a longitudinal canal in the Wolffian body, but this could not be clearly seen. In the segment immediately behind the last vas efferens was a fully developed segmental tube. This embryo clearly throws no light on the question at issue except that on the whole it supports Semper's views. I further failed to make out anything from an examination of still younger embryos.

In a somewhat older embryo there was connected with the anterior vas efferens a peculiar structure represented on Pl. XIX. fig. 7, *r. st?* which strangely resembled the opening of an ordinary segmental tube, but as I could not find it in the younger embryo, this suggestion as to its nature, is, at the best, extremely hazardous. If, however, this body really is the remnant of a segmental opening, it would be reasonable to conclude that the vasa efferentia are buds from the segmental tubes as opposed to their openings; a mode of origin which is not incompatible with the discoveries of Dr Spengel. I have noticed a remnant, somewhat similar to that in the Scyllium embryo, close to the hindermost vas efferens in an embryo Squatina (Pl. XIX. fig. 8, *r.st?*).

With reference to the development of the longitudinal canal of the Wolffian body, I am without observations, but it appears to me to be probably a further development of the outgrowths of the vesicles of each segmental tube, which were described in connection with the development of the segmental tubes, p. 262. Were an anterior outgrowth of one vesicle to meet and coalesce with the posterior outgrowth of the preceding vesicle, a longitudinal canal such as actually exists would be the result. The central canal of the base of the testes and the network connected with it in the adult (Pl. XIX. fig. 4), appear to be derivatives of the vasa efferentia.

I am thus compelled to leave open the question of the real nature of the vasa efferentia, but am inclined to regard them as outgrowths from the anterior segmental tubes, though not from their open terminations.

* * *

My views upon the homologies of the various parts of the urinogenital system, the development of which has been described in the present chapter, have already been expressed in a paper on Urinogenital organs of Vertebrates[1]. Although Kolliker's[2] discovery of the segmental tubes in Aves, and the researches of Spengel[3], Gasser[4], Ewart[5] and others, have ren-

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[1] *Journal of Anatomy and Physiology*, Vol. x.

[2] *Entwicklungsgeschichte des Menschen u. der höheren Thiere.*

[3] *Loc. cit.*

[4] *Beiträge zur Entwicklungsg. d. Allantois d. Müller'schen Gänge u. d. Afters.*

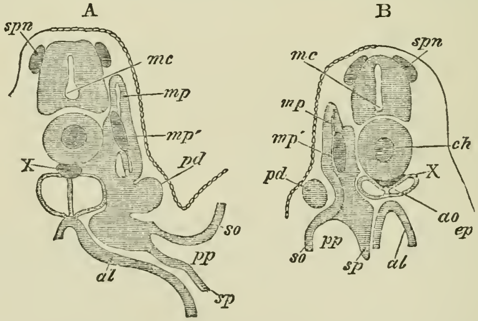
[5] Abdominal Pores and Urogenital Sinus of Lamprey, *Journal of Anatomy and Physiology*, Vol. x. p. 488.

dered necessary a few corrections in my facts, I still adhere in their entirety to the views expressed in that paper, and feel it unnecessary to repeat them in this place. I conclude the chapter with a résumé of the development of the urinogenital organs in Elasmobranchs from their first appearance to their permanent condition.

Résumé.—The first trace of the urinary system makes its appearance as a knob springing from the intermediate cell-mass opposite the fifth protovertebra (woodcut, fig. 5A *p.d*). This knob is the rudiment of the abdominal opening of the segmental duct, and from it there grows backwards to the level of the anus a solid column of cells, which constitutes the rudiment of the segmental duct itself (woodcut, fig. 5B *p.d*). The knob projects towards the epiblast, and the column connected with it lies between the mesoblast and epiblast. The knob and column do not long remain solid, but the former acquires an opening into the body-cavity continuous with a lumen, which makes its appearance in the latter.

Fig. 5.

Two Sections of a Pristiurus Embryo with three visceral clefts.



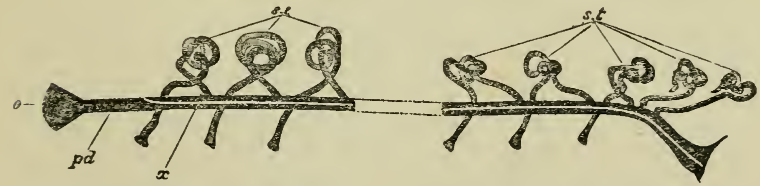
The sections illustrate the development of the segmental duct (*pd.*) or primitive duct of the kidneys. In *A* (the anterior of the two sections) this appears as a solid knob (*pd*) projecting towards the epiblast. In *B* is seen a section of the column which has grown backwards from the knob in *A*.

spn. rudiment of a spinal nerve; *mc.* medullary canal; *ch.* notochord; *X.* string of cells below the notochord; *mp.* muscle-plate; *mp′.* specially developed portion of muscle-plate; *ao.* dorsal aorta; *pd.* segmental duct. *so.* somatopleure; *sp.* splanchnopleure; *pp.* pleuroperitoneal or body-cavity; *ep.* epiblast; *al.* alimentary canal.

While the lumen is gradually pushing its way backwards along the solid rudiment of the segmental duct, the first traces of the segmental tubes, or proper excretory organs, make their appearance in the form of solid outgrowths of the intermediate cell-mass, which soon become hollow and open into the body-cavity. Their blind ends curl obliquely backwards round the inner and dorsal side of the segmental duct. One segmental tube makes its appearance for each protovertebra, commencing with that immediately behind the abdominal opening of the segmental duct, the last tube being situated a short way behind the anus. Soon after their formation the blind ends of the segmental tubes open into the segmental duct, and each of them becomes divided into four parts. These are (woodcut 7) (1) a section carrying the abdominal opening or segmental tube proper, (2) a dilated vesicle into which this opens, (3) a coiled tubulus proceeding from (2) and terminating in (4), a wider portion opening into the segmental duct. At the same time, or shortly before this, each segmental duct unites with and opens into one of the horns of the cloaca, and also retires from its primitive position between the epiblast and mesoblast, and assumes a position close to the epithelium lining the body-cavity.

Fig. 6.

Diagram of the primitive condition of the Kidney in an Elasmobranch Embryo.



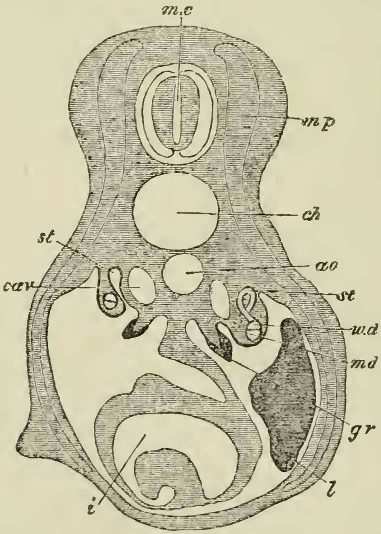
pd. segmental duct. It opens at *o* into the body-cavity and at its other extremity into the cloaca; *x.* line along which the division appears which separates the segmental duct into the Wolffian duct above and the Müllerian duct below; *st.* segmental tubes. They open at one end into the body-cavity, and at the other into the segmental duct.

The general features of the excretory organs at this period are diagrammatically represented on the woodcut, fig. 6. In this fig. *p.d* is the segmental duct and *o* its abdominal opening. *s.t* points to the segmental tubes, the finer details of whose structure are not represented in the diagram. The kidneys thus form at this period an unbroken gland composed of a series of isolated coiled tubes, one extremity of each of which opens into the body-cavity, and the other into the segmental duct, which forms the only duct of the kidney, and communicates at one end with the body-cavity, and at the other with the cloaca.

The next important change concerns the segmental duct, which becomes longitudinally split into two complete ducts in the female, and one complete duct and parts of a second in the male. The manner in which this takes place is diagrammatically represented in woodcut 6 by the clear line *x*, and in transverse section in woodcut 7. The resulting ducts are

Fig. 7.

DIAGRAMMATIC REPRESENTATION OF A TRANSVERSE SECTION OF A SCYLLIUM EMBRYO ILLUSTRATING THE FORMATION OF THE WOLFFIAN AND MULLERIAN DUCTS BY THE LONGITUDINAL SPLITTING OF THE SEGMENTAL DUCT.



mc. medullary canal; *mp.* muscle-plate; *ch.* notochord; *ao.* aorta; *ca v.* cardinal vein; *st.* segmental tube. On the one side the section passes through the opening of a segmental tube into the body-cavity. On the other this opening is represented by dotted lines, and the opening of the segmental tube into the Wolffian duct has been cut through; *w.d.* Wolffian duct; *m.d.* Müllerian duct. The section is taken through the point where the segmental duct and Wolffian duct have just become separate; *gr.* The germinal ridge with the thickened germinal epithelium; *l.* liver; *i.* intestine with spiral valve.

the (1) Wolffian duct dorsally, which remains continuous with the excretory tubules of the kidney, and ventrally (2) the oviduct or Müllerian duct in the female, and the rudiments of this duct in the male. In the female the formation of these ducts takes place by a nearly solid rod of cells, being gradually split off from the ventral side of all but the foremost part of the original segmental duct, with the short undivided anterior part of which duct it is continuous in front. Into it a very small portion of the lumen of the original segmental duct is perhaps continued (Pl. XX. fig. 1 A, etc.). The remainder of the segmental duct (after the loss of its anterior section and the part split off from its ventral side) forms the Wolffian duct. The process of formation of the ducts in the male chiefly differs from that in the female in the fact of the anterior undivided part of the segmental duct, which forms the front end of the Müllerian duct, being shorter, and in the column of cells with which it is continuous being from the first incomplete.

The tubuli of the primitive excretory organ undergo further important changes. The vesicle at the termination of each segmental tube grows forwards towards the preceding tubulus, and joins the fourth section of it close to the opening into the Wolffian duct (Pl. XX. fig. 10). The remainder of the vesicle becomes converted into a Malpighian body. By the first of these changes a connection is established between the successive segments of the kidney, and though this connection is certainly lost (or only represented by fibrous bands) in the anterior part of the excretory organs in the adult, and very probably in the hinder part, yet it seems most probable that traces of it are to be found in presence of the secondary Malpighian bodies of the majority of segments, which are most likely developed from it.

Up to this time there has been no distinction between the anterior and posterior tubuli of the primitive excretory organ which alike open into the Wolffian duct. The terminal division of the tubuli of a considerable number of the hindermost of these (ten or eleven in Scyllium canicula), either in some species elongate, overlap, and eventually open by apertures (not usually so numerous as the separate tubes), on nearly the same level, into the hindermost section of the Wolffian duct in the female, or into the urinogenital cloaca, formed by the coalesced terminal parts of the Wolffian ducts, in the male; or in other species become modified in such a manner as to pour their secretion into a single duct on each side, which opens in a position corresponding with the numerous ducts of the other type (woodcut, fig. 8). It seems that both in Amphibians and Elasmobranchs the type with a single duct, or approximations to it, are more often found in the females than in the males. The subject requires however to be more worked out in Elasmobranchs[1]. In both groups the modified posterior kidney-segments are probably equivalent to the permanent kidney of the amniotic Vertebrates, and for this reason the numerous ducts of the first group or single duct of the second were spoken of as ureters. The anterior tubuli of the primitive excretory organ retain their early relation to the Wolffian duct, and form the Wolffian body.

The originally separate terminal extremities of the Wolffian ducts always coalesce, and form a urinal cloaca, opening by a single aperture situated at the extremity of median papilla behind the anus. Some of the abdominal openings of the segmental tubes in Scyllium, or in other cases all the openings, become obliterated.

In the male the anterior segmental tubes undergo remarkable modifications. There appear to grow from the first three or four or more of them (though the point is still somewhat obscure) branches, which pass to base of the testis and there unite into a longitudinal canal, form a network, and receive the secretion of the testicular ampullæ (woodcut 9, *nt*). These ducts, the vasa efferentia, carry the semen to the Wolffian body, but before opening into the tubuli of this they unite into the *longitudinal canal of the Wolffian body* (*l.c*), from which pass off ducts equal in number to the vasa efferentia, each of which normally ends in a Malpighian body. From the Malpighian body so connected start the convoluted tubuli of what may be called the generative segments of the Wolffian body along

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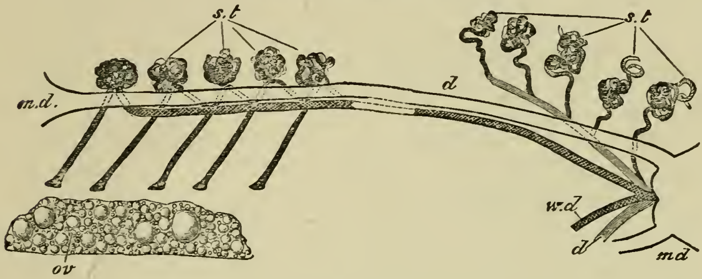
[1] The reverse of the above rule is the case with Raja, in the male of which a closer approximation to the single-duct type is found than in the female.

which the semen is conveyed to the Wolffian duct (*v. d*). The Wolffian duct itself becomes much contorted and acts as vas deferens.

Fig. 8.

Diagram of the arrangement of the Urinogenital Organs in an adult Female Elasmobranch.



m.d. Müllerian duct; *w.d.* Wolffian duct; *s.t.* glandular tubuli; five of them are represented with openings into the body-cavity; *d.* duct of the posterior segmental tubes; *ov.* ovary.

In the woodcuts, fig. 8 and 9, are diagrammatically represented the chief constituents of the adult urinogenital organs in the two sexes. In the adult female, fig. 8, there are present the following parts:

(1) The oviduct or Müllerian duct (*m.d*) split off from the segmental duct of the kidneys. Each oviduct opens at its anterior extremity into the body-cavity, and behind the two oviducts have independent communications with the general cloaca.

(2) The Wolffian ducts (*w.d*), the other product of the segmental ducts of the kidneys. They end in front by becoming continuous with the tubulus of the anterior segment of the Wolffian body on each side, and unite behind to open by a common papilla into the cloaca. The Wolffian duct receives the secretion of the anterior part of the primitive kidney which forms the Wolffian body.

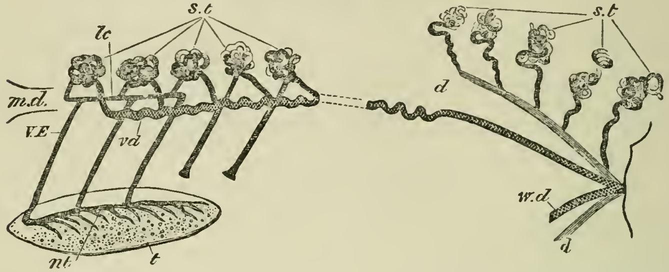
(3) The ureter (*d*) which carries off the secretion of the kidney proper. It is represented in my diagram in its most rare and differentiated condition as a single duct.

(4) The glandular tubuli (*s.t*), some of which retain their original opening into the body-cavity, and others are without them. They are divided into two groups, an anterior forming

the Wolffian body, which pour their secretion into the Wolffian duct, and a posterior group forming the kidney proper, which are connected with the ureter.

Fig. 9.

Diagram of the Arrangement of the Urinogenital Organs in an Adult Male Elasmobranch.



m.d. rudiment of Müllerian duct; *w.d.* Wolffian duct, marked *vd* in front and serving as vas deferens; *st.* glandular tubuli; two of them are represented with openings into the body-cavity; *d.* ureter; *t.* testis; *nt.* central canal at the base of the testis; *VE.* vasa efferentia; *lc.* longitudinal canal of the Wolffian body.

In the male the following parts are present (woodcut 9):

(1) The Müllerian duct (*md*), consisting of a small rudiment attached to the liver representing the foremost end of the oviduct of the female.

(2) The Wolffian duct (*w.d*) which precisely corresponds to the Wolffian duct of the female, but, in addition to functioning as the duct of the Wolffian body, also acts as a vas deferens (*vd*). In the adult male its foremost part has a very tortuous course.

(3) The ureter (*d*), which has the same fundamental constitution as in the female.

(4) The segmental tubes (*st*). The posterior of these have the same arrangement in both sexes, but in the male modifications take place in connection with the anterior ones to fit them to act as transporters of the testicular products.

Connected with the anterior ones there are present (1) the vasa efferentia (VE), united on the one hand with (2) the central canal in the base of the testis (*nt*), and on the other with the longitudinal canal of the Wolffian body (*l.c*). From the latter are seen passing off the successive tubuli of the anterior segments of the Wolffian body in connection with which Malpighian bodies are typically present, though not represented in my diagram.

Postscript.

It was my original intention to have given an account of the development of the generative organs. In the course, however, of my work a number of novel and unexpected points turned up, which have considerably protracted my investigations, and it has appeared to me better no longer to delay the appearance of this monograph, but to publish elsewhere my results on the generative organs. In chapter VI. p. 130 *et seq.* the early stages of the generative organs are described, but in contemplation of the completion of the account no allusion was made to their literature, and more especially to Professor Semper's important contributions. I may perhaps say that I have been able to confirm the most important result to which he and other anatomists have nearly simultaneously arrived with respect to Vertebrates, viz. *that the primitive ova give rise to both the male and female generative products.*

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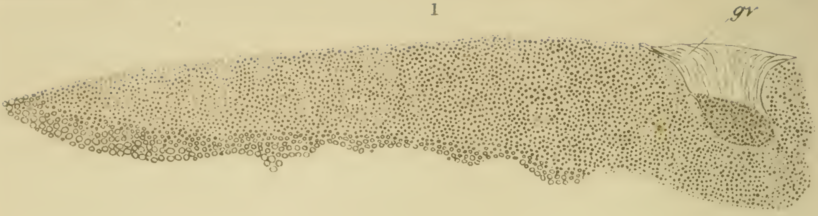

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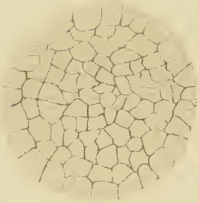

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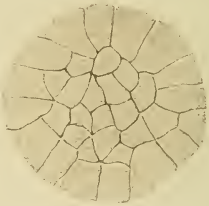

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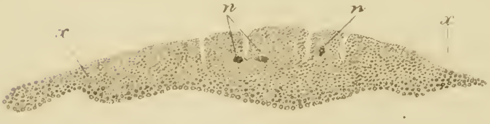


6c

6a

6b

Collings

[illegible] Lith.
188, Strand, London. W.C.

EXPLANATION OF PLATE I.

Fig. 1. Section through the germinal disc of a ripe ovarian ovum of the Skate. *gv.* germinal vesicle.

Fig. 2. Surface-view of a germinal disc with two furrows.

Figs. 3, 4, 5. Surface-views of three germinal discs in different stages of segmentation.

Fig. 6. Section through the germinal disc represented in fig. 3. *n.* nucleus; *x.* edge of germinal disc. The engraver has not accurately copied my original drawings in respect to the structure of the segmentation furrows.

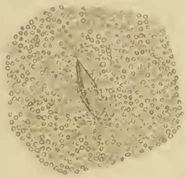
Figs. 6 *a* and 6 *b*. Two furrows of the same germinal disc more highly magnified.

Fig. 6 *c*. A nucleus from the same germinal disc highly magnified.

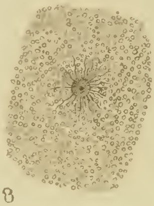
Pl. II

7

7a



7b



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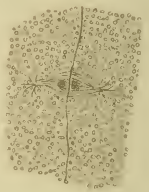


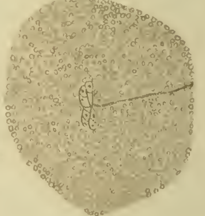
8

8a

8b

8c

8d



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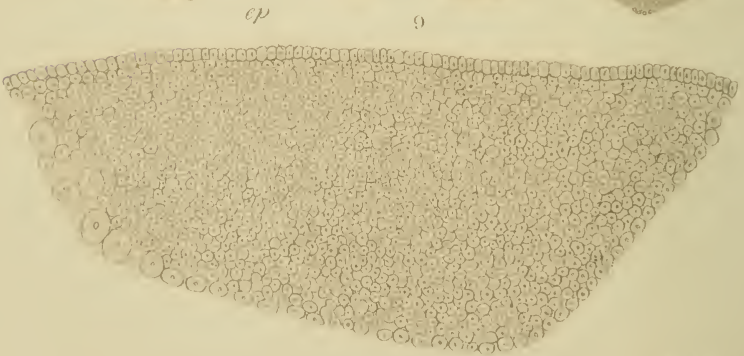


F P Collings

[illegible] lith. [illegible]

EXPLANATION OF PLATE II.

Fig. 7. Section through a germinal disc of the same age as that represented in fig. 4. *n.* nucleus; *nx.* modified nucleus; *nx'.* modified nucleus of the yolk; *f.* furrow appearing in the yolk around the germinal disc.

Figs. 7*a*, 7*b*, 7*c*. Three segments with modified nuclei from the same germinal disc.

Fig. 8. Section through a somewhat older germinal disc. *ep.* epiblast; *n'.* nuclei of the yolk.

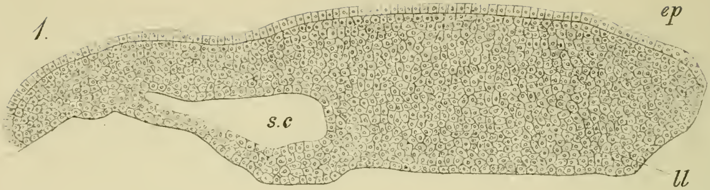
Figs. 8 *a*, 8 *b*, 8 *c*. Modified nuclei from the yolk from the same germinal disc.

Fig. 8 *d*. Segment in the act of division from the same germinal disc.

Fig. 9. Section through a germinal disc in which the segmentation is completed. It shows the larger collection of cells at the embryonic end of the germinal disc than at the non-embryonic. *ep.* epiblast.

III,

1.



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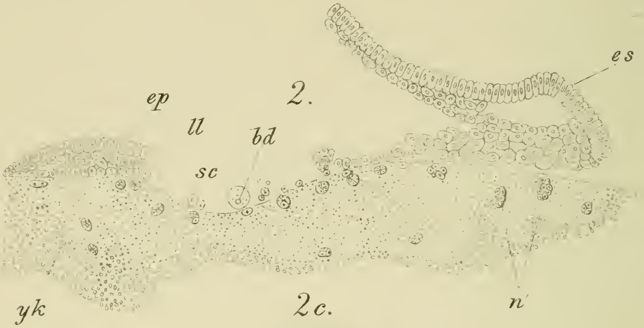
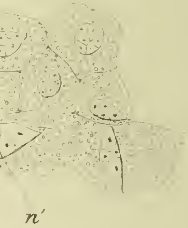


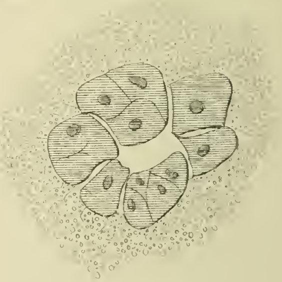
2c.

2a.



3.

2b.



4.

5.

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EXPLANATION OF PLATE III.

ep. epiblast.
ll. lower layer cell.
m. mesoblast.
hy. hypoblast.
sc. segmentation cavity.
es. embryo swelling.
n'. nuclei of yolk.

1. Longitudinal section of a blastoderm at the first appearance of the segmentation cavity.

2. Longitudinal section through a blastoderm after the layer of cells has disappeared from the floor of the segmentation cavity. *bd.* large cell resting on the yolk, probably remaining over from the later periods of segmentation. Magnified 60 diameters. (Hardened in chromic acid.)

The section is intended to illustrate the fact that the nuclei form a layer in the yolk under the floor of the segmentation cavity. The roof of the segmentation cavity is broken.

2 *a.* Portion of same blastoderm highly magnified, to show the characters of the nuclei of the yolk *n'* and the nuclei in the cells of the blastoderm.

2 *b.* Large knobbed nucleus from the same blastoderm, very highly magnified.

2 *c.* Nucleus of yolk from the same blastoderm.

3. Longitudinal section of blastoderm of same stage as fig. 2. (Hardened in chromic acid.)

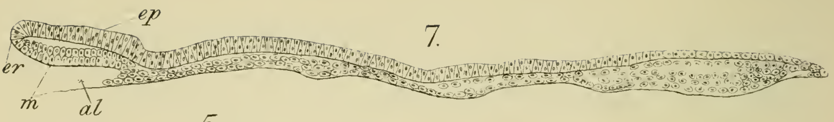
4. Longitudinal section of blastoderm slightly older than fig. 2. Magnified 45 diameters. (Hardened in osmic acid.)

It illustrates (1) the characters of the epiblast; (2) the embryonic swelling; (3) the segmentation cavity.

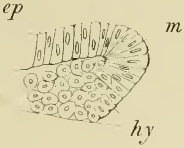
5. Longitudinal section through a blastoderm at the time of the first appearance of the embryonic rim, and before the formation of the medullary groove. Magnified 45 diameters.

IV

7.



5. a.



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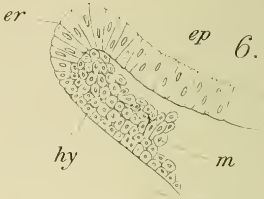
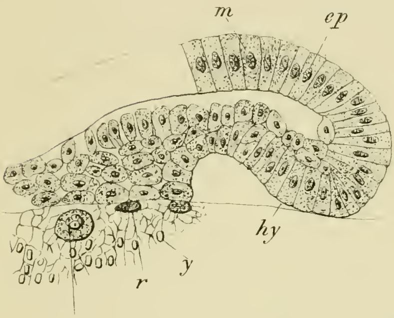
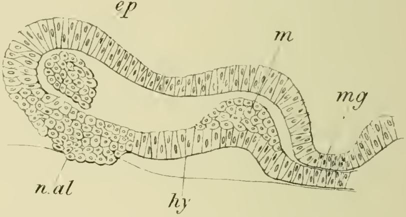


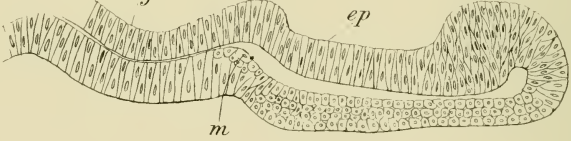
7. a.



8. b.



8. c.



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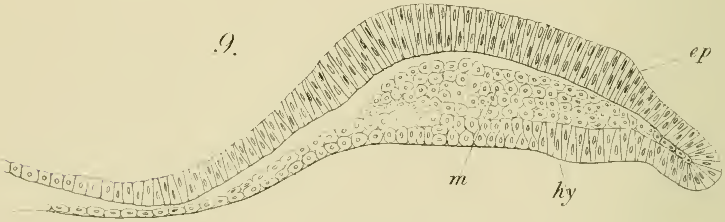
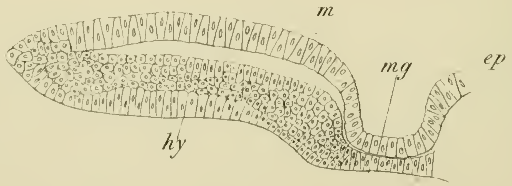


8. a.



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EXPLANATION OF PLATE IV.

ep. epiblast.

m. mesoblast.

hy. hypoblast.

er. embryonic rim.

n. al. cells formed around the nuclei of the yolk which have entered the hypoblast.

c. cell formed around nucleus of yolk.

mg. medullary groove.

5 *a.* Section through the periphery of the embryonic rim of the blastoderm of which fig. 5 represents a section.

6. Section through the embryonic rim of a blastoderm somewhat younger than that represented on Pl. VI. fig. B.

7. Section through the most projecting portion of the embryonic rim of a blastoderm of the same age as that represented on Pl. VI. fig. B. The section is drawn on a very considerably smaller scale than that on Pl. III. fig. 5. It is intended to illustrate the growth of the embryonic rim and the disappearance of the segmentation cavity.

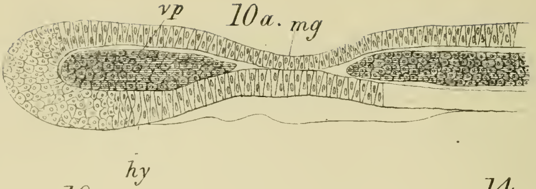
7 *a.* Section through peripheral portion of the embryonic rim of the same blastoderm, highly magnified. It specially illustrates the formation of a cell (*c*) around a nucleus in the yolk. The nuclei of the blastoderm have been inaccurately rendered by the artist.

8 *a*, 8 *b*, 8 *c*. Three sections of the same embryo. Inserted mainly to illustrate the formation of the mesoblast as two independent lateral masses of cells; only half of each section is represented. 8 *a* is the most posterior of the three sections. In it the mesoblast forms a large mass on each side, imperfectly separated from the hypoblast. In 8 *b*, from the anterior part of the embryo, the main mass of mesoblast is far smaller, and only forms a cap to the hypoblast at the highest point of the medullary fold. In 8 *c* a cap of mesoblast is present, similar to that in 8 *b*, though much smaller. The sections of these embryos were somewhat oblique, and it has unfortunately happened that while in 8 *a* one side is represented, in 8 *b* and 8 *c* the other side is figured, had it not been for this the sections 8 *b* and 8 *c* would have been considerably longer than 8 *a*.

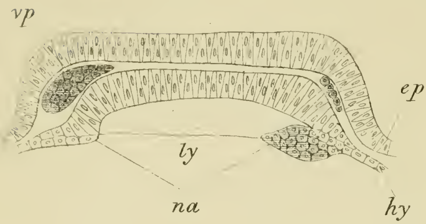
9. Longitudinal section of an embryo belonging to a slightly later stage than B.

This section passes through one of the medullary folds. It illustrates the continuity of the hypoblast with the remaining lower layer cells of the blastoderm.

10 a.



10 c.



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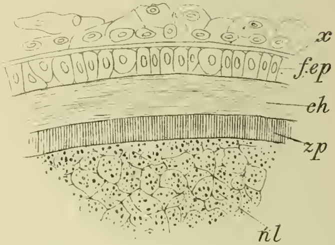
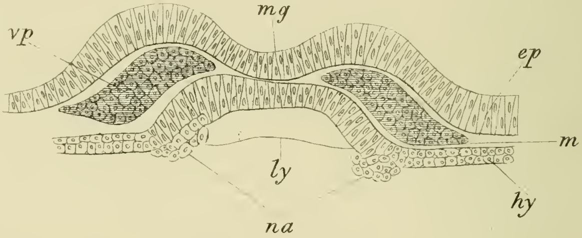


10 b.



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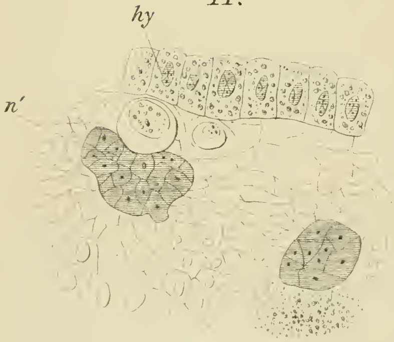
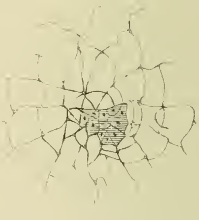


12.



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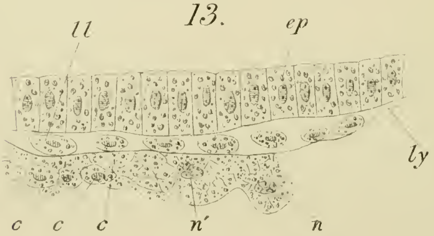


T. P. Collings.

EXPLANATION OF PLATE V.

ep. epiblast.
m. mesoblast.
hy. hypoblast.
vp. combined lateral and vertebral plate of mesoblast.
na. cells to form ventral wall of alimentary canal which have been derived from the yolk.
ly. line separating the yolk from the blastoderm.
mg. medullary groove.
n'. nucleus of yolk.
c. cells formed in the yolk around the nuclei of the yolk.

10 *a*, 10 *b*, 10 *c*. Three sections of the same embryo belonging to a stage slightly later than B, Pl. VI. The space between the mesoblast and the hypoblast has been made considerably too great in the figures of the three sections.

10 *a*. The most posterior of the three sections. It shows the posterior flatness of the medullary groove and the two isolated vertebral plates.

10 *b*. This section is taken from the anterior part of the same embryo and shows the deep medullary groove and the commencing formation of the ventral wall of the alimentary canal from the nuclei of the yolk.

10 *c* shows the disappearance of the medullary groove and the thinning out of the mesoblast plates in the region of the head.

11. Small portion of the blastoderm and the subjacent yolk of an embryo at the time of the first appearance of the medullary groove × 300. It shows two large nuclei of the yolk (*n*) and the protoplasmic network in the yolk between them; the network is seen to be closer round the nuclei than in the intervening space. There are no areas representing cells around the nuclei.

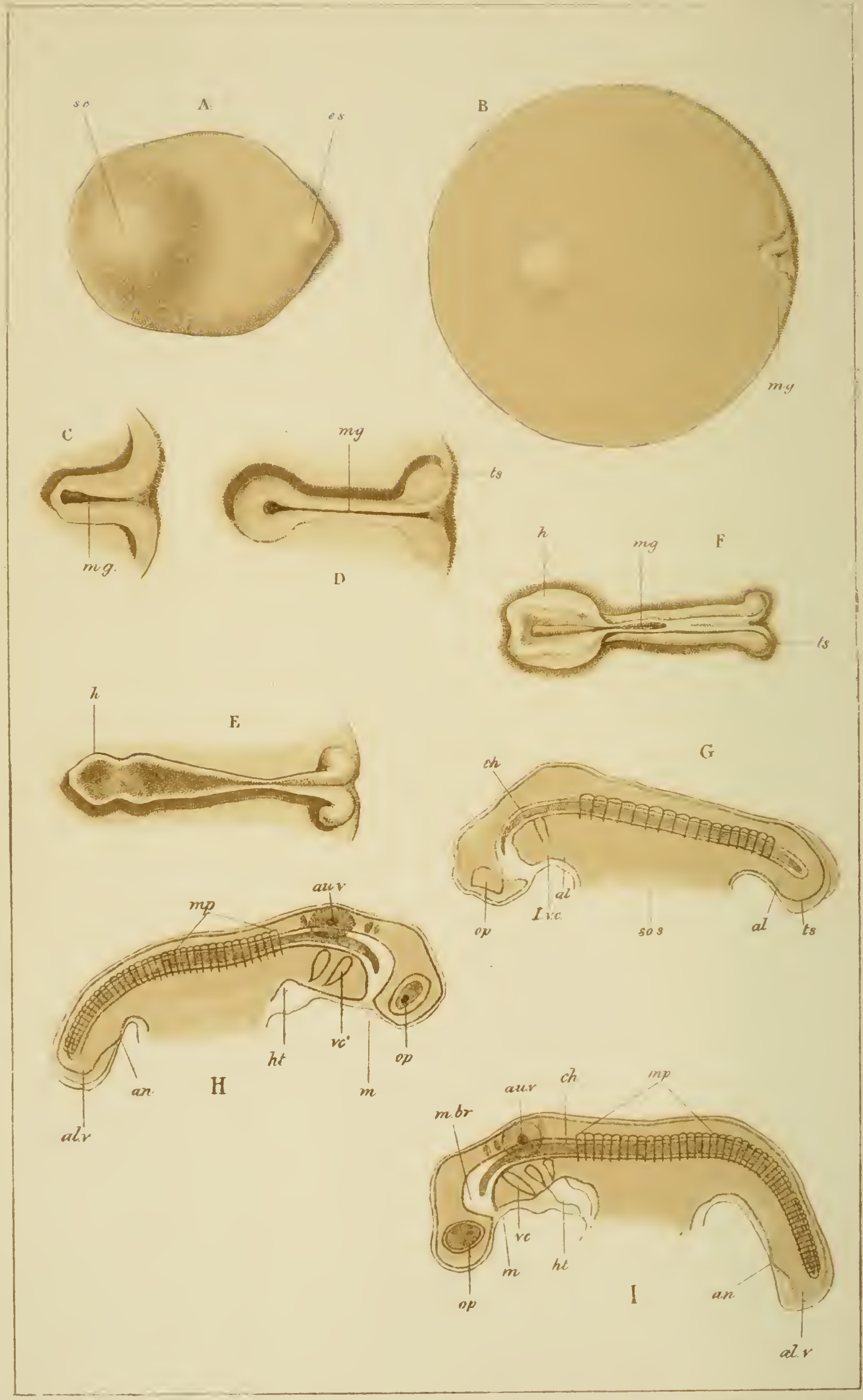
12. Nucleus of the yolk in connection with the protoplasmic network hardened in osmic acid.

13. Portion of posterior end of a blastoderm of stage B, showing the formation of cells around the nuclei of the yolk.

14. Section through part of a young Scyllium egg, about $\frac{1}{15}$th of an inch in diameter.

n. l. protoplasmic network in yolk.
z. p. zona pellucida.
ch. structureless chorion.
f. ep. follicular epithelium.
x. structureless membrane external to this.

Pl VI



Cooper & Hodson Lith

88, Strand, London, W.C.

EXPLANATION OF PLATE VI.

s. c.	segmentation cavity.
es.	embryo-swelling.
mg.	medullary groove.
ts.	tail-swelling.
h.	head.
ch.	notochord.
op.	eye.
au. v.	auditory vesicle.
al.	alimentary cavity.
so. s.	somatic stalk.
I. *v. c.*	1st visceral cleft.
vc.	visceral cleft.
mp.	muscle-plate or protovertebræ.
m.	mouth.
an.	point where anus will appear.
al. v.	alimentary vesicle at the posterior end of the alimentary canal.
ht.	heart.

A. Surface view of blastoderm of Pristiurus hardened in chromic acid.

B. Surface view of fresh blastoderm of Pristiurus.

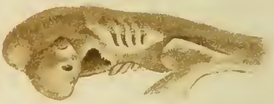
C, D, E, and F. Pristiurus embryos hardened in chromic acid.

G. Torpedo embryo viewed as a transparent object.

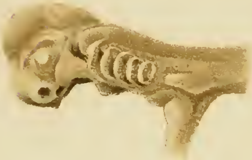
H, I. Pristiurus embryos viewed as transparent objects.

K × 5½

× 3 L



L′ × 5



× 5 M

M′ × 5

× 3 N

N′ × 5

× 1½ O

O′ × 3

× 1½ P

Q × 1½

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EXPLANATION OF PLATE VII.

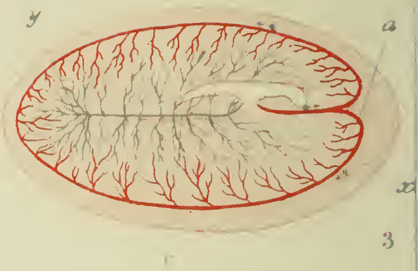
K. Pristiurus embryo hardened in chromic acid.

The remainder of the figures are representations of embryos of Scyllium canicula hardened in chromic acid. In every case, with the exception of the figures marked P and Q, two representations of the same embryo are given; one from the side and one from the under surface.

VII

1

2



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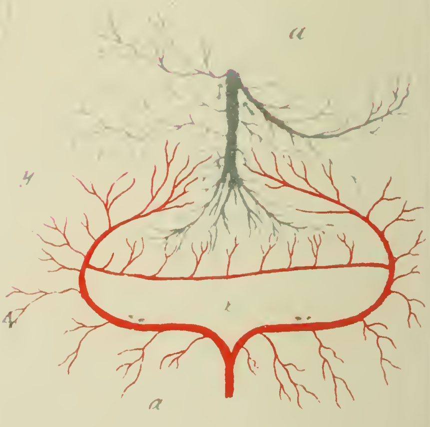


4

EXPLANATION OF PLATE VIII.

yk. yolk.

bl. blastoderm.

a. arteries of yolk sac (red).

v. veins of yolk sac (blue).

x. portion of blastoderm outside the arterial circle in which no blood-vessels are present.

1. Yolk of a Pristiurus egg with blastoderm and embryo. About two-thirds of the yolk has been enveloped by the blastoderm. The embryo is still situated at the edge of the blastoderm, but at the end of a bay in the outline of this. The thickened edge of the blastoderm is indicated by a darker shading. Two arteries have appeared.

2. Yolk of an older Pristiurus egg. The yolk has become all but enveloped by the blastoderm, and the embryo ceases to lie at the edge of the blastoderm, owing to the coalescence of the two sides of the bay which existed in the earlier stage. The circulation is now largely developed. It consists of an external arterial ring, and an internal venous ring, the latter having been developed in the thickened edge of the blastoderm. Outside the arterial ring no vessels are developed.

3. The yolk has now become completely enveloped by the blastoderm. The arterial ring has increased in size. The venous ring has vanished, owing to the complete enclosure of the yolk by the blastoderm. The point where it existed is still indicated (*y*) by the brush-like termination of the main venous trunk in a number of small branches.

4. Diagrammatic projection of the vascular system of the yolk sac of a somewhat older embryo.

The arterial ring has grown much larger and the portion of the yolk where no vessels exist is very small (*x*). The brush-like termination of the venous trunk is still to be noticed.

The two main trunks (arterial and venous) in reality are in close contact as in fig. 5, and enter the somatic stalk close together.

The letter *a* which points to the venous (blue) trunk should be *v* and not *a*.

5. Circulation of the yolk sac of a still older embryo, in which the arterial circle has ceased to exist, owing to the space outside it having become smaller and smaller and finally vanished.

IX

Fig. 1 a

Fig. 3 a

Fig 3b

Fig. 1 b

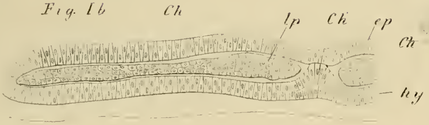


Fig. 3 c

Fig 3 d

Fig. 1 c

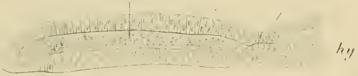


Fig 3 e

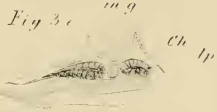


Fig. 3. f.

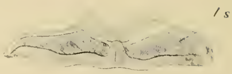


Fig 2

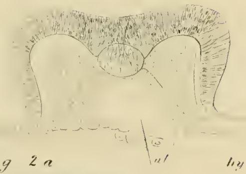


Fig. 5

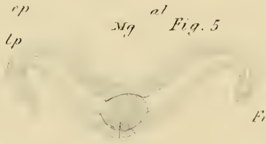


Fig. 4

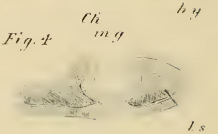


Fig. 8

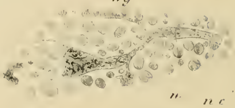


Fig 2 a

Fig. 2 b

Fig 2 c

Fig 6

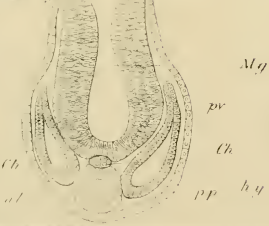


Fig 7

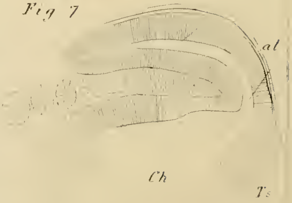


Fig. 3

F M Balfour

T P Collings

EXPLANATION OF PLATE IX.

ep. epiblast. *hy.* hypoblast.

l p. coalesced lateral and vertebral plate of mesoblast.

m g. medullary groove. *n c.* neural or medullary canal.

p v. protovertebra. *so.* somatopleure.

sp. splanchnopleure. *t s.* mesoblast of tail-swelling.

ch. chorda dorsalis or notochord.

ch'. ridge of hypoblast, which will become separated off as the notochord.

al. alimentary canal.

n. a. cells formed around the nuclei of the yolk to enter into the ventral wall of the alimentary canal.

n. nucleus of yolk. *yk.* yolk spherules.

Fig. 1 *a.* 1 *b.* 1 *c.* Three sections from the same embryo belonging to a stage intermediate between B and C, of which fig. 1 *a* is the most anterior. × 96 diameters.

The sections illustrate (1) The different characters of the medullary groove in the different regions of the embryo. (2) The structure of the coalesced lateral and vertebral plates. (3) The mode of formation of the notochord as a thickening of the hypoblast (*ch'*), which eventually becomes separated from the hypoblast as an elliptical rod (1 *a. ch*).

Fig. 2. Section through the anterior part of an embryo belonging to stage *C.* The section is mainly intended to illustrate the formation of the ventral wall of the alimentary canal from cells formed around the nuclei of the yolk. It also shews the shallowness of the medullary groove in the anterior part of the body.

Fig. 2 *a.* 2 *b.* 2 *c.* Three sections from the same embryo as fig. 2 Fig. 2 *a* is the most anterior of the three sections and is taken through a point shortly in front of fig. 2. The figures illustrate the general features of an embryo of stage *C*, more especially the complete closing of the alimentary canal in front and the triangular section which it there presents.

Fig. 3. Section through the posterior part of an embryo belonging to stage *D.* × 86 diameters.

It shews the general features of layer during the stage, more especially the differentiation of somatic and splanchnic layers of the mesoblast.

Fig. 3 *a.* 3 *b.* 3 *c.* 3 *d.* 3 *e.* 3 *f.* Sections of the same embryo as fig. 3 (× 60 diameters). Fig. 3 belongs to part of the embryo intermediate between fig. 3 *e* and 3 *f.*

The sections shew the features of various parts of the embryo. Fig. 3 *a.* 3 *b.* and 3 *c.* belong to the head, and special attention should be paid to the presence of a cavity in the mesoblast in 3 *b* and to ventral curvature of the medullary folds.

Fig. 3 *d* belongs to the neck, fig. 3 *e* to the back, and fig. 3 *f* to the tail.

Fig. 4. Section through the region of the tail at the commencement of stage F. × 60 diameters.

The section shews the character of the tail-swellings and the commencing closure of the medullary groove.

Fig. 5. Transverse section through the anterior part of the head of an embryo belonging to stage F. (× 60 diameters). It shews (1) the ventral curvature of the medullary folds next the head. (2) The absence of mesoblast in the anterior part of the head. *hy* points to the extreme front end of the alimentary canal.

Fig. 6. Section through the head of an embryo at a stage intermediate between F and G. × 86 diameters.

It shews the manner in which the medullary folds of the head unite to form the medullary canal.

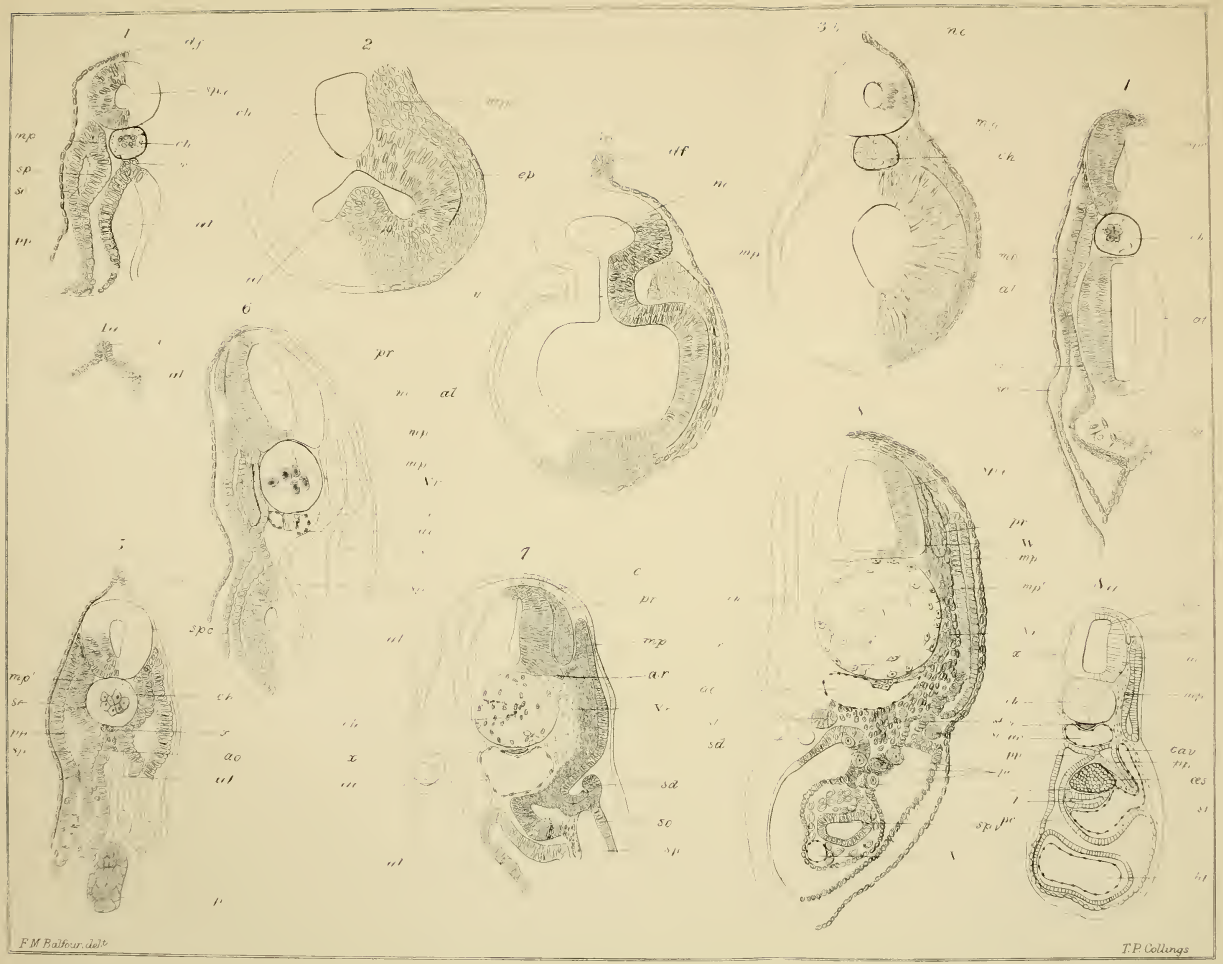
Fig. 7. Longitudinal and vertical section through the tail of an embryo belonging to stage G.

It shews the direct communication which exists between the neural and alimentary canals.

The section is not quite parallel to the long axis of the embryo, so that the protovertebræ are cut through in its anterior part, and the neural canal passes out of the section anteriorly.

Fig. 8. Network of nuclei from the yolk of an embryo belonging to stage H.

Plate X.



F.M. Balfour, del^t

T.P. Collings

EXPLANATION OF PLATE X.

Complete list of reference letters.

ep. epiblast. *df.* dorsal fin. *sp. c.* spinal cord.
W. white matter of spinal cord. *nc.* neural canal.
pr. posterior root of spinal nerve.
ar. anterior root of spinal nerve. *mp.* muscle-plate.
mp'. early formed band of muscles from the splanchnic layer of the muscle-plates.
Vr. vertebral rudiment. *so.* somatic layer of mesoblast.
sp. splanchnic layer of mesoblast. *pp.* body-cavity.
pc. pericardial cavity. *c.* connective-tissue cells.
sd. segmental duct. *st.* segmental tube. *po.* primitive ovum.
ao. dorsal aorta. *ca v.* cardinal vein. *sv.* sinus venosus.
ht. heart. *v.* splanchnic vein. *ch.* notochord.
x. subnotochordal rod. *al.* alimentary tract. *sp. v.* spiral valve.
y. passage connecting the neural and alimentary canals.
l. liver. *p.* protoplasm from yolk in the alimentary tract.

Fig. 1. Section from the caudal region of a Pristiurus embryo belonging to stage H. Zeiss C. Ocul. 1. Osmic acid specimen.

It shews (1) the constriction of the subnotochordal rod (*x*) from the summit of the alimentary canal. (2) The formation of the body-cavity in the muscle-plate and the ventral thickening of the parietal plate.

Fig. 1*a*. Portion of alimentary wall of the same embryo, shewing the formation of the subnotochord rod (*x*).

Fig. 2. Section through the caudal vesicle of a Pristiurus embryo belonging to stage H. Zeiss C. Ocul. 1.

It shews the bilobed condition of the alimentary vesicle and the fusion of the mesoblast and hypoblast at the caudal vesicle.

Fig. 3*a*. Sections from the caudal region of a Pristiurus embryo belonging to stage H. Zeiss C. Ocul. 1. Picric acid specimen.

It shews the communication which exists posteriorly between the neural and alimentary canals, and also by comparison with 3*b* it exhibits the dilatation undergone by the alimentary canal in the caudal vesicle.

Fig. 3*b*. Section from the caudal region of an embryo slightly younger than 3*a*. Zeiss C. Ocul. 1. Osmic acid specimen.

Fig. 4. Section from the cardiac region of a Pristiurus embryo belonging to stage H. Zeiss C. Ocul. 1. Osmic acid specimen.

It shews the formation of the heart (*ht*) as a cavity between the splanchnopleure and the wall of the throat.

Fig. 5. Section from the posterior dorsal region of a Scyllium embryo, belonging to stage H. Zeiss C. Ocul. 1. Osmic acid specimen.

It shews the general features of an embryo of stage H, more especially the relations of the body-cavity in the parietal and vertebral portions of the lateral plate, and the early formed band of muscle (*mp'*) in the splanchnic layer of the vertebral plate.

Fig. 6. Section from the œsophageal region of Scyllium embryo belonging to stage I. Zeiss C. Ocul. 1. Chromic acid specimen.

It shews the formation of the rudiments of the posterior nerve-roots (*pr*) and of the vertebral rudiments (*Vr*).

Fig. 7. Section of a Torpedo embryo belonging to stage slightly later than I. Zeiss C. Ocul. 1. reduced $\frac{1}{3}$. Osmic acid specimen.

It shews (1) the formation of the anterior and posterior nerve-roots. (2) The solid knob from which the segmental duct (*sd*) originates.

Fig. 8. Section from the dorsal region of a Scyllium embryo belonging to a stage intermediate between I and K. Zeiss C. Ocul. 1. Chromic acid specimen.

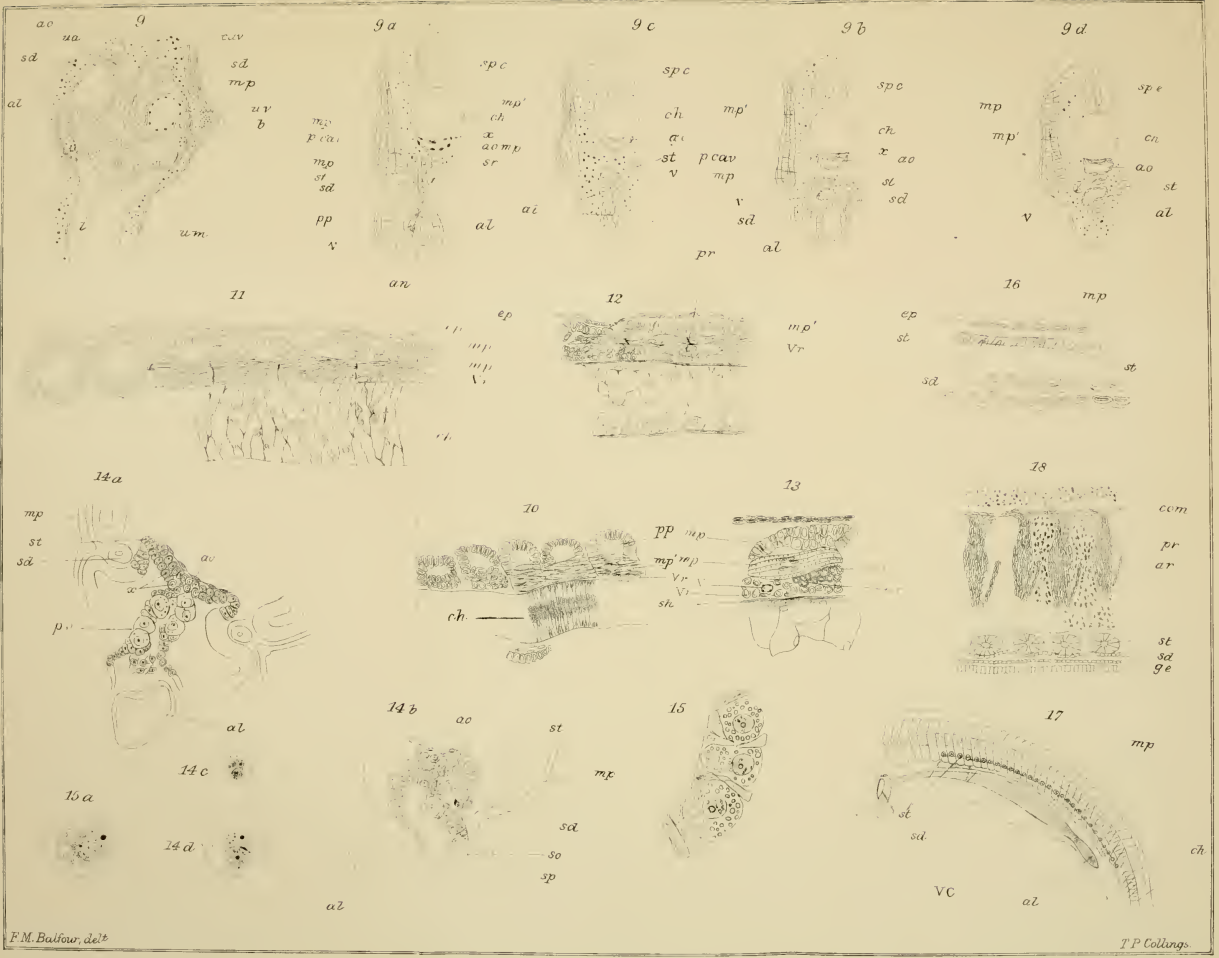
It illustrates the structure of the primitive ova, segmental tubes, notochord, etc.

Fig. 8*a*. Section from the caudal region of an embryo of the same age as 8. Zeiss A. Ocul. 1.

It shews (1) the solid œsophagus. (2) The narrow passage connecting the pericardial (*pc*) and body cavities (*pp*).

XI

Plate XI.



F.M. Balfour, delt

T P Collings.

EXPLANATION OF PLATE XI.

Complete list of reference letters.

ep. epiblast. *sp. c.* spinal canal.
pr. rudiment of posterior root of spinal nerve.
ar. „ „ anterior root of spinal nerve.
b. anterior fin. *mp.* muscle-plate.
mp'. early formed band of muscles. *Vr.* vertebral rudiment.
pp. body-cavity. *um.* umbilical cord. *sd.* segmental duct.
st. segmental tube. *sr.* inter-renal body. *po.* primitive ovum.
ge. germinal epithelium. *vc.* visceral cleft. *ao.* dorsal aorta.
ca v. cardinal vein. *v.* splanchnic vein.
ua. umbilical artery. *uv.* umbilical vein.
v. blood-vessel. *ch.* notochord.
sh. cuticular sheath of notochord. *x.* subnotochordal rod (except in fig. 14 *a*).
al. alimentary tract. *l.* liver.
an. point where anus will be formed.

Fig. 9. Section of a Pristiurus embryo belonging to stage K. Zeiss A. Ocul. 1. Osmic acid specimen.

It shews the formation of the liver (*l*), the structure of the anterior fins (*b*), and the anterior opening of the segmental duct into the body-cavity (*sd*).

Fig. 9*a*, 9*b*, 9*c*, 9*d*. Four sections through the anterior region of the same embryo as 9. Osmic acid specimens.

The sections shew (1) the atrophy of the post-anal section of the alimentary tract (9*b*, 9*c*, 9*d*). (2) The existence of the segmental tubes behind the anus (9*b*, 9*c*, 9*d*). With reference to these it deserves to be noted that the segmental tubes behind the anus are quite disconnected, as is proved by the fact that a tube is absent on one side in 9*c* but reappears in 9*d*. (3) The downward prolongation of the segmental duct to join the posterior or cloacal extremity of the alimentary tract (9*b*).

Fig. 10. Longitudinal and horizontal section of a Scyllium embryo of stage H. Zeiss C. Ocul. 1. Reduced by $\frac{1}{3}$. Picric acid specimen.

It shews (1) the structure of the notochord ; (2) the appearance of the early formed band of muscles (*mp'*.) in the splanchnic layer of the protovertebra.

Fig. 11. Longitudinal and horizontal sections of an embryo belonging to stage I. Zeiss C. Ocul. 1. Chromic acid specimen. It illustrates the same points as the previous section, but in addition shews the formation of the rudiments of the vertebral bodies (*Vr*) which are seen to have the same segmentation as the muscle-plates.

Fig. 12.[1] Longitudinal and horizontal section of an embryo belonging to the stage intermediate between I and K. Zeiss C. Ocul. 1. Osmic acid specimen illustrating the same points as the previous section.

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[1] The apparent structure in the sheath of the notochord in this and the succeeding figure is merely the result of an attempt on the part of the engraver to represent the dark colour of the sheath in the original figure.

Fig. 13. Longitudinal and horizontal section of an embryo belonging to stage K, Zeiss C. Ocul. 1, and illustrating same points as previous section.

Fig. 14*a*, 14*b*, 14*c*, 14*d*. Figures taken from preparations of an embryo of an age intermediate between I and K, and illustrating the structure of the primitive ova. Fig. 14*a* and 14*b* are portions of transverse sections. Zeiss C. Ocul. 3 reduced $\frac{1}{3}$. Fig. 14*c* and 14*d* are individual ova, shewing the lobate form of nucleus. Zeiss F. Ocul. 2.

Fig. 15. Osmic acid preparation of primitive ova belonging to stage K. Zeiss immersion No. 2, Ocul. 1. The protoplasm of the ova is seen to be nearly filled with bodies resembling yolk-spherules: and one ovum is apparently undergoing division.

Fig. 15*a*. Picric acid preparation shewing a primitive ovum partially filled with bodies resembling yolk-spherules.

Fig. 16. Horizontal and longitudinal section of Scyllium embryo belonging to stage K. Zeiss A. Ocul. 1. Picric acid preparation. The connective-tissue cells are omitted.

The section shews that there is one segmental tube to each vertebral segment.

Fig. 17. Portion of a Scyllium embryo belonging to stage K, viewed as a transparent object.

It shews the segmental duct and the segmental involutions—two of which are seen to belong to segments behind the end of the alimentary tracts.

Fig. 18. Vertical longitudinal section of a Scyllium embryo belonging to stage K. Zeiss A. Ocul. 1. Hardened in a mixture of osmic and chromic acid. It shews

(1) the commissures connecting together the posterior roots of the spinal nerves;
(2) the junction of the anterior and posterior roots;
(3) the relations of the segmental ducts to the segmental involutions and the alternation of calibre in the segmental tube;
(4) the germinal epithelium lining the body-cavity.

XII

Pl. XII

EXPLANATION OF PLATE XII.

Complete list of reference letters.

ep. epiblast. *sp. c.* spinal cord. *l l.* lateral line.
sp. g. spinal ganglion. *m. c.* mucous canal of the head.
n. l. nervus lateralis. *v. in.* intestinal branch of the vagus.
v. op. ramus ophthalmicus of the fifth nerve.
m. p. muscle-plate. *m. p'.* muscles of muscle-plate.
v. ar. vertebral arch. *na.* neural arch. *ha.* hæmal arch.
rp. rib process. *m. el.* membrana elastica externa.
v b. vertebral body. *ch.* notochord. *sh.* sheath of notochord.
x. sub-notochordal rod. *sy. g.* sympathetic ganglion.
s. d. segmental duct. *l.* liver. *al.* alimentary tract.
um. ductus choledochus. *ao.* aorta. *ca v.* cardinal vein.
v. cau. caudal vein. *v.* blood-vessel. *c.* connective tissue.

Fig. 1. Section through the anterior part of an embryo of *Scyllium canicula* during stage L.

c. Peculiar large cells which are found at the dorsal part of the spinal cord. Sympathetic ganglion shewn at *sy. g.* Zeiss A, ocul. 1.

Fig. 2. Section through the lateral line at the time of its first formation. The cells marked *n. l.* were not sufficiently distinct to make it quite certain that they really formed part of the lateral nerve. Zeiss B, ocul. 2.

Fig. 3*a*. 3*b*. 3*c*. 3*d*. Four sections of the lateral line from an embryo belonging to stage L. 3*a* is the most anterior. In 3*a* the lateral nerve (*n. l.*) is seen to lie in the mesoblast at some little distance from the lateral line. In 3*b* and 3*c* it lies in immediate contact with and partly enclosed by the modified epiblast cells of the lateral line. In 3*d*, the hindermost section, the lateral line is much larger than in the other sections, but no trace is present of the lateral nerve. The sections were taken from the following slides of my series of the embryo (the series commencing at the tail end) 3*d* (46). 3*c* (64). 3*b* (84). 3*a* (93). The figures all drawn on the same scale, but 3*a* is not from the same side of the body as the other sections.

Fig. 4. Section through lateral line of an embryo of stage P at the point where it is acquiring an opening to the exterior. The peculiar modified cells of its innermost part deserve to be noticed. Zeiss D, ocul. 2.

Fig. 5. Mucous canals of the head with branches of the ramus ophthalmicus growing towards them. Stage O. Zeiss A, ocul. 2.

Fig. 6. Mucous canals of head with branches of the ramus ophthalmicus growing towards them. Stage between O and P. Zeiss *aa*, ocul. 2.

Fig. 7. Junction of a nerve and mucous canal. Stage P. Zeiss D, ocul. 2.

Fig. 8. Longitudinal and horizontal section through the muscle-plates and adjoining structures at a stage intermediate between L and M. The section is intended to shew the gradual conversion of the cells of the somatic layer of muscle-plates into muscles.

Fig. 9. Longitudinal section through the notochord and adjoining parts to shew the first appearance of the cartilaginous notochordal sheath which forms the vertebral centra. Stage N.

Fig. 10. Transverse section through the tail of an embryo of stage P to shew the coexistence of the rib-process and hæmal arches in the first few sections behind the point where the latter appear. Zeiss C, ocul. 1.

Fig. 11. Transverse section through the centre of a caudal vertebra of an embryo somewhat older than Q. It shews (1) the similarity between the arch-tissue and the hyaline tissue of the outer layer of the vertebral centrum, and (2) the separation of the two by the membrana elastica externa[1]. (*m. el*) It shews also the differentiation of three layers in the vertebral centrum: vide p. 153.

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[1] The slight difference observable between these two tissues in the arrangement of their nuclei has been much exaggerated by the engraver.

XIII

Plate XIII.

Fig. 1.

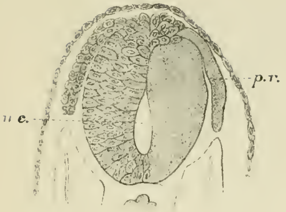


Fig. 2.

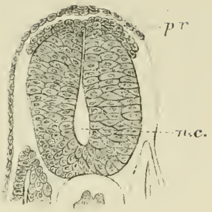


Fig. 3.

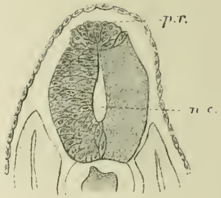


Fig. 4.

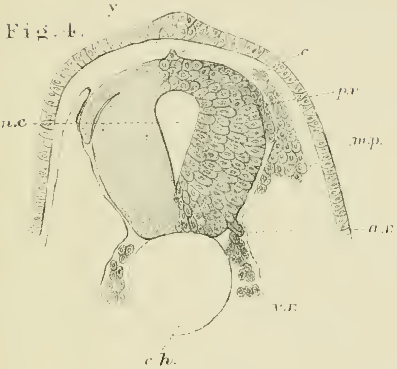


Fig. 5.

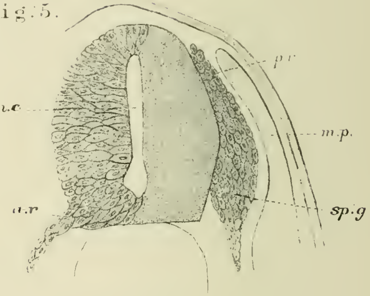


Fig. 6.

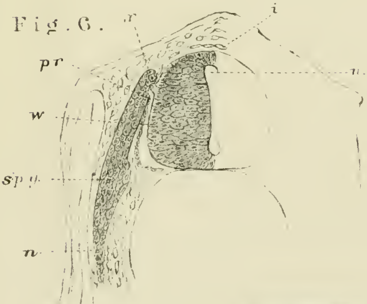


Fig. 7.

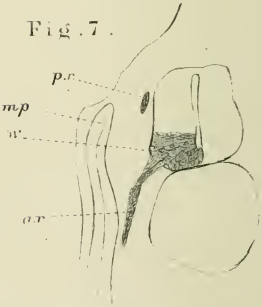


Fig. 8.

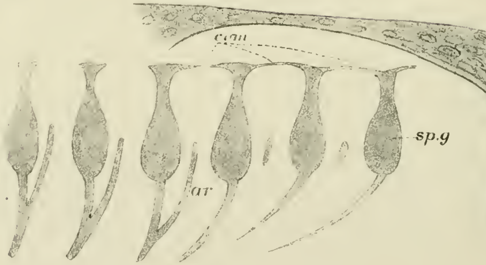
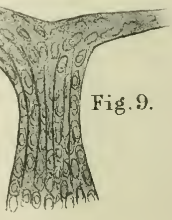


Fig. 9.



F.M.Balfour

T.P. Collings.

EXPLANATION OF PLATE XIII.

This Plate illustrates the Formation of the Spinal Nerves.

Complete list of reference letters.

p r. posterior root of a spinal nerve.
a r. anterior root of a spinal nerve. *n.* spinal nerve.
sp g. ganglion on posterior root of spinal nerve.
com. commissure connecting the posterior roots of the spinal nerves.
w. white matter of spinal cord. *n.c.* neural canal.
y. point where the spinal cord became segmented off from the superjacent epiblast.
i. mesoblastic investment of spinal cord. *m.p.* muscle-plate.
v.r. vertebral rudiment. *ch.* notochord.

Fig. 1, 2, and 3. Three sections of a Pristiurus embryo belonging to stage I. Fig. 1 passes through the heart, fig. 2 through the anterior part of the dorsal region, fig. 3 through a point slightly behind this. (Zeiss CC, ocul. 2.) In fig. 3 there is visible a slight proliferation of cells from the dorsal summit of the neural canal. In fig. 2 this proliferation definitely constitutes two club-shaped masses of cells (*p r*)—the rudiments of the posterior nerve-roots,—both attached to the dorsal summit of the spinal cord. In fig. 1 the rudiments of the posterior roots are of considerable length.

Fig. 4. Section through the dorsal region of a Torpedo embryo slightly older than stage I, with three visceral clefts. (Zeiss CC, ocul. 2.) The section shews the formation of a pair of dorsal nerve-rudiments (*p r*) and a ventral nerve-rudiment (*a r*). The latter is shewn in its youngest condition, and is not distinctly cellular.

Fig. 5. Section through the dorsal region of a Torpedo embryo slightly younger than stage K. (Zeiss CC, ocul. 2.) The connective-tissue cells are omitted. The rudiment of the ganglion (*sp. g.*) on the posterior root has appeared, and the junction of posterior root with the cord is difficult to detect. The anterior root forms an elongated cellular structure.

Fig. 6. Section through the dorsal region of a Pristiurus embryo of stage K. (Zeiss CC, ocul. 2.) The section especially illustrates the attachment of the posterior root to the spinal cord.

Fig. 7. Section through the same embryo as fig. 6. (Zeiss CC, ocul. 1.) The section contains an anterior root, which takes its origin at a point opposite the interval between two posterior roots.

Fig. 8. A series of posterior roots with their central ends united by a dorsal commissure, from a longitudinal and vertical section of a Scyllium embryo belonging to a stage intermediate between L and M. The embryo was hardened in a mixture of osmic and chromic acids.

Fig. 9. The central end of a posterior nerve-root from the same embryo, with the commissure springing out from it on either side.

XIV

Fig. 1.

Fig 2.

Fig 3.

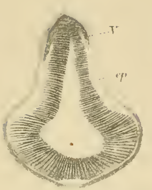


Fig 4b.

Fig 4a.

Fig. 5b.

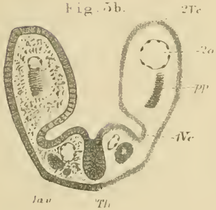


Fig 5a

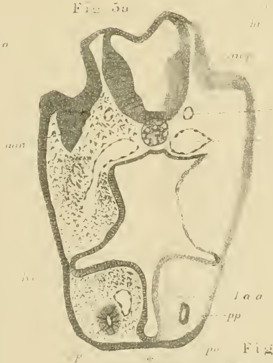
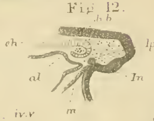


Fig 12.



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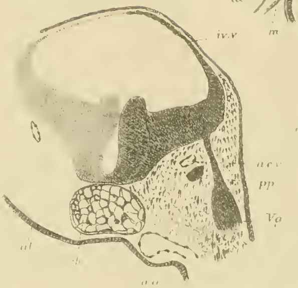

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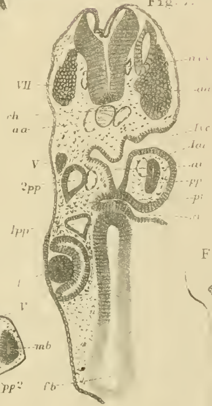

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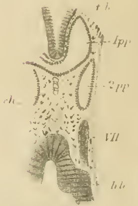

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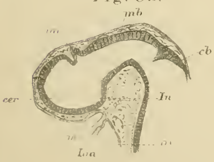

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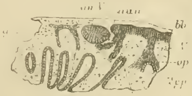


Fig. 11.

Fig. 16a.

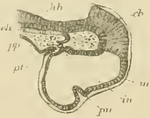


Fig. 16b.

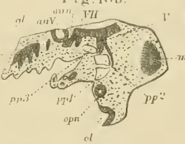


Fig. 13a.

Fig. 9b

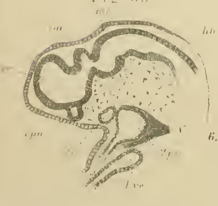
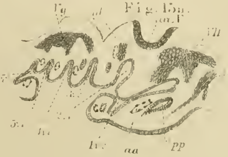


Fig. 15a.



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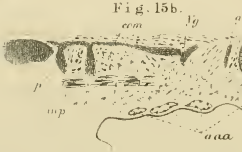

Fig. 14.

Fig. 13b.

F.M Balfour

T.P Collings.

EXPLANATION OF PLATE XIV.

THE HEAD DURING STAGES G—K.

Complete list of references.

e p. external epiblast. *op.* eye. *op. v.* optic vesicle.
op. n. optic nerve. *l.* lens. *Ch.* choroid slit.
hy. hyaloid membrane. *ol.* olfactory pit. *au. v.* auditory vesicle.
au. n. auditory nerve. *au. p.* auditory pit.
au. thickening of epiblast to form the auditory pit.
f b. fore-brain. *cer.* cerebrum. *pn.* pineal gland.
pt. pituitary body. *In.* infundibulum.
m b. mid-brain. *b b.* base of brain. *b.* wall of brain.
h b. hind-brain. *cb.* cerebellum. iv. *v.* fourth ventricle.
sp. c. spinal cord.
v. fifth nerve. *opth.* v. ophthalmic branch of fifth. *mn.* v. mandibular branch of fifth. vii. seventh or facial nerve. *gl.* glossopharyngeal nerve. *com.* commissure connecting roots of vagus nerve.
Vg. vagus. *p.* posterior root of spinal nerve.
1, 2 etc. *p p.* first, second, etc. section of body cavity in the head.
ch. notochord.
m. mesoblast at the base of the brain.
ht. heart. *V. c.* visceral cleft. 1, 2, 3 etc. *e.g.* external gills.
al. alimentary canal. *Th.* thyroid body.
ao. aorta. 1 *a. a.* 2 *a. a.* etc. 1st, 2d, etc. aortic arch.
a. c. v. anterior cardinal vein. *v.* blood-vessel.
M. mouth involution.
so. somatopleure. *sp.* splanchnopleure.

Fig. 1. Head of a Pristiurus embryo of stage K viewed as a transparent object.

The points which deserve special attention are: (1) The sections of the body cavity in the head (*pp.*). The first or premandibular section being situated close to the eye. The second in the mandibular arch. Above this one the fifth nerve bifurcates. The third at the summit of the hyoid arch.

The cranial nerves and the general appearance of the brain are well shewn in the figure.

The notochord cannot be traced in the living embryo so far forward as it is represented. It has been inserted according to the position which it is seen to occupy in sections.

Fig. 2. Head of an embryo of Scyllium canicula somewhat later than stage K, viewed as a transparent object.

The figure shews the condition of the brain; the branches of the fifth and seventh nerves (v. vii.); the rudiments of the semicircular canals; and the commencing appearance of the external gills as buds on both walls of 2nd, 3rd, and 4th clefts. The external gills have not appeared on first cleft or spiracle.

Fig. 3. Section through the head of a Pristiurus embyro during stage G. It shews (1) the fifth nerve (v.) arising as an outgrowth from the dorsal summit of the brain. (2) The optic vesicles not yet constricted off from the fore-brain.

Fig. 4 *a* and 4 *b*. Two sections through the head of a Pristiurus embryo of stage I. They shew (1) the appearance of the seventh nerve. (2) The portion of the body cavity belonging to the first and second visceral arches. (3) The commencing thickening of epiblast to form the auditory involution.

In 4 *b*, the posterior of the two sections, no trace of an auditory nerve is to be seen.

Fig. 5 *a* and 5 *b*. Two sections through the head of a Torpedo embryo with 3 visceral clefts. Zeiss A, ocul. 1.

5 *a* shews the formation of the thin roof of the fourth ventricle by a divarication of the two lateral halves of the brain.

Both sections shew the commencing formation of the thyroid body (*th*) at the base of the mandibular arch.

They also illustrate the formation of the visceral clefts by an outgrowth from the alimentary tract without any corresponding ingrowth of the external epiblast.

Fig. 6. Section through the hind-brain of a somewhat older Torpedo embryo. Zeiss A, ocul. 1.

The section shews (1) the attachment of a branch of the vagus to the walls of the hind-brain. (2) The peculiar form of the hind-brain.

Fig. 7. Transverse section through the head of a Pristiurus embryo belonging to a stage intermediate between I and K, passing through both the fore-brain and the hind-brain. Zeiss A, ocul. 1.

The section illustrates (1) the formation of the pituitary body (*pt*) from the mouth involution (*m*), and proves that, although the wall of the throat (*al*) is in contact with the mouth involution, there is by this stage no communication between the two. (2) The eye. (3) The sections of the body cavity in the head, 1 *pp*. 2 *pp*. (4) The fifth nerve (v.) and the seventh nerve (vii.).

Fig. 8. Transverse section through the brain of a rather older embryo than fig. 7. It shews the ventral junction of the anterior sections of the body cavity in the head, 1 *pp*.

Fig. 9 *a* and 9 *b*. Two longitudinal sections through the brain of a Pristiurus embryo belonging to a stage intermediate between I and K. (Zeiss A, ocul. 1.)

Fig. 9 *a* is taken through the median line, but is reconstructed from two sections. It shews (1) The divisions of the brain—The cerebrum and thalamencephalon in the fore-brain; the mid-brain; the commencing cerebellum in the hind-brain. (2) The relation of the mouth involution to the infundibulum. (3) The termination of the notochord.

Fig. 9 *b* is a section to one side of the same brain. It shews (1) The divisions of the brain. (2) The point of outgrowth of the optic nerves, *op. n.* (3) The sections of the body cavity in the head and the bifurcation of the optic nerve over the 2nd of these.

Fig. 10. Longitudinal section through the head of a Pristiurus embryo somewhat younger than fig. 9. Zeiss a, ocul. 4. It shews the relation of the nerves and the junction of the fifth, seventh, and auditory nerves with the brain.

Fig. 11. Longitudinal section through the fore-brain of a Pristiurus embryo of stage K, slightly to one side of the middle line. It shews the deep constriction separating the thalamencephalon from the cerebral hemispheres.

Fig. 12. Longitudinal section through the base of the brain of an embryo of a stage intermediate between I and K.

It shews (1) The condition of the end of the notochord. (2) The relation of mouth involution to the infundibulum.

Fig. 13 *a*. Longitudinal and horizontal section through part of the head of a Pristiurus embryo rather older than K. Zeiss A, ocul. 1.

The figure contains the eye cut through in the plane of the choroid slit. Thus the optic nerve (*op. n*) and choroid slit (*ch*) are both exhibited. Through the latter is seen passing mesoblast accompanied by a blood-vessel (*v*). *Op* represents part of the optic vesicle to one side of the choroid slit.

No mesoblast can be seen passing round the outside of the optic cup; and the only mesoblast which enters the optic cup passes through the choroid slit.

Fig. 13 *b*. Transverse section through the last arch but one of the same embryo as 13 *a*. Zeiss A, ocul. 1.

The figure shews (1) The mode of formation of a visceral cleft without any involution of the external skin. (2) The head cavity in the arch and its situation in relation to the aortic arch.

Fig. 14. Surface view of the nasal pit of an embryo of same age as fig. 13, considerably magnified. The specimen was prepared by removing the nasal pit, flattening it out and mounting in glycerine after treatment with chromic acid. It shews the primitive arrangement of the Schneiderian folds. One side has been injured.

Fig. 15 *a* and 15 *b*. Two longitudinal and vertical sections through the head of a Pristiurus embryo belonging to stage K. Zeiss a, ocul. 3.

Fig. 15 *a* is the most superficial section of the two. It shews the constitution of the seventh and fifth nerves, and of the intestinal branch of the vagus. The anterior branch of the seventh nerve deserves a special notice.

Fig. 15 *b* mainly illustrates the dorsal commissure of the vagus nerve (*com*) continuous with the dorsal commissures of the posterior root of the spinal nerves.

Fig. 16. Two longitudinal and vertical sections of the head of a Pristiurus embryo belonging to the end of stage K. Zeiss a, ocul. 1.

Fig. 16 *a* passes through the median line of the brain and shews the infundibulum, notochord and pituitary body, etc.

The pituitary body still opens into the mouth, though the septum between the mouth and the throat is broken through.

Fig. 16 *b* is a more superficial section shewing the head cavities *pp*. 1, 2, 3, and the lower vagus commissure.

XV

EXPLANATION OF PLATE XV.

Complete list of references.

cer. cerebral hemispheres. *ch.* notochord.
l v. lateral ventricle. *p cl.* posterior clinoid.
pn. pineal gland. *mn.* mandible.
x. rudiment of septum which will grow backwards and divide the unpaired cerebral rudiment into the two hemispheres.
c in. internal carotid. *op. n.* optic nerve.
op. eye. *in.* infundibulum. *pt.* pituitary body.
ol. olfactory pit. *ol. l.* olfactory lobe.
op. th. optic thalamus. *p c.* posterior commissure.
m b. mid-brain, or optic lobes. *cb.* cerebellum.
md. medulla oblongata. iv. *v.* fourth ventricle.
f t. fasciculi teretes. *r t.* restiform tracts.
t v. tela vasculosa of the roof of the fourth ventricle.
au. v. auditory vesicle. vii. seventh nerve.

Fig. 1 *a*, 1 *b*, 1 *c*. Longitudinal sections of the brain of a Scyllium embryo belonging to stage L. Zeiss a, ocul. 1.

1 *a* is taken slightly to one side of the middle line, and shews the general features of the brain, and more especially the infundibulum (*in.*) and pituitary body (*pt*).

1 *b* is through the median line of the pineal gland.

1 *c* is through the median line of the base of the brain, and shews the notochord (*ch.*) and pituitary body (*pt*); the latter still communicating with the mouth. It also shews the wide opening into the infundibulum in the middle line of the base of the brain.

Fig. 2. Section through the unpaired cerebral rudiment during stage O, to shew the origin of the olfactory lobe and the olfactory nerve. The latter is seen to divide into numerous branches, one of which passes into each Schneiderian fold. At its origin are numerous ganglion cells represented by dots. Zeiss a, ocul. 2.

Fig. 3. Horizontal section through the three lobes of the brain during stage O. Zeiss a, ocul. 2.

The figure shews (1) the very slight indications which have appeared by this stage of an ingrowth to divide the cerebral rudiment into two lobes, *x.* (2) The optic thalami united by a posterior commissure, and on one side joining the base of the mid-brain, and behind them the pineal gland. (3) The thin posterior wall of the cerebral rudiment with folds projecting into the cerebral cavity.

Fig. 4 *a*, 4 *b*, 4 *c*. Views from the side, from above, and from below, of a brain of Scyllium canicula during stage P. In the view from the side the eye (*op.*) has not been removed.

The bilobed appearance both of the mid-brain and cerebellum should be noticed.

Fig. 5. Longitudinal section of a brain of Scyllium canicula during stage P. Zeiss a, ocul. 2.

There should be noticed (1) the increase in the flexure of the brain accompanying a rectification of the cranial axis; (2) the elongated pineal gland, and (3) the structure of the optic thalamus.

Fig. 6 *a*, 6 *b*, 6 *c*. Views from the side, from above, and from below, of a brain of Scyllium stellare during a slightly later stage than Q.

Fig. 7 *a* and 7 *b*. Two longitudinal sections through the brain of a Scyllium embryo during stage Q. Zeiss a, ocul. 2.[1]

7 *a* cuts the hind part of the brain nearly through the middle line; while 7 *b* cuts the cerebral hemispheres and pineal gland through the middle.

In 7 *a* the infundibulum (1), cerebellum (2), the passage of the restiform tracts (*r t*) into the cerebellum (3), and the rudiments of the tela vasculosa (4) are shewn. In 7 *b* the septum between the two lobes of the cerebral hemispheres (1), the pineal gland (2), and the relations of the optic thalami (3) are shewn.

Fig. 8 *a*, 8 *b*, 8 *c*, 8 *d*. Four transverse sections of the brain of an embryo slightly older than Q. Zeiss a, ocul. 1.

8 *a* passes through the cerebral hemispheres at their junction with the olfactory lobes. On the right side is seen the olfactory nerve coming off from the olfactory lobe. At the dorsal side of the hemispheres is seen the pineal gland (*pn*).

8 *b* passes through the mid-brain now slightly bilobed, and the opening into the infundibulum (*in*). At the base of the section are seen the optic nerves and their chiasma.

8 *c* passes through the opening from the ventricle of the mid-brain into that of the cerebellum. Below the optic lobes is seen the infundibulum with the rudiments of the sacci vasculosi.

8 *d* passes through the front end of the medulla, and shews the roots of the seventh pair of nerves, and the overlapping of the medulla by the cerebellum.

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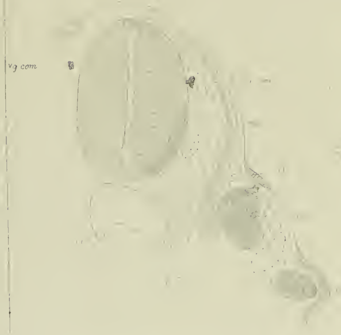
[1] Owing to a mistake of the engravers the references to the pituitary body are *pr* in 7 *a* and *pn* in 7 *b*. They should be *pt* in both cases.

XVI.

3



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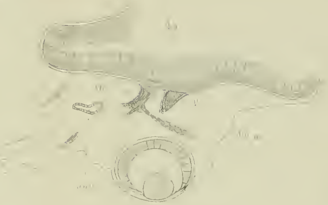

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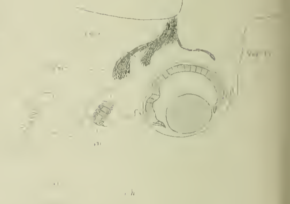

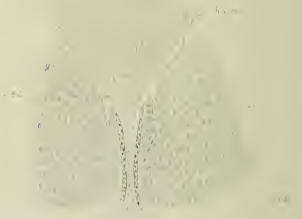

EXPLANATION OF PLATE XVI.

Complete list of references.

v. fifth nerve.
v. *op. th.* ramus ophthalmicus of fifth nerve.
v. *mx.* „ maxillæ superioris of fifth nerve.
v. *mn.* „ mandibularis of fifth nerve.
vii. seventh nerve.
vii. *mn.* mandibular (spiracular) branch of seventh nerve.
vii. *hy.* hyoid branch of seventh nerve.
vii. *a.* anterior branch of seventh nerve.
gl. glossopharyngeal nerve. *vg.* vagus nerve.
vg. r. roots of vagus nerves in the brain.
vg. com. commissure uniting the roots of the vagus, and continuous with commissure uniting the posterior roots of the spinal nerves.
vg. in. intestinal branch of vagus.
vg. br. branchial branch of vagus.
n l. nervus lateralis. *p r.* posterior root of spinal nerve.
a r. anterior root of spinal nerve. *v c.* visceral cleft.
sp. spiracle. *au. v.* auditory vesicle. *op.* eye.
ol. olfactory pit. *cer.* cerebrum. *ch.* notochord.
p ch. parachordal cartilage. *l l.* lateral line.
pp. head cavity. *hy. m.* hyaloid membrane.
p fal. processus falciformis. *rt.* retina.
ch. epithelial layer of choroid membrane. *v h.* vitreous humour.

Fig. 1. Diagram of cranial nerves at stage L.

A description of the part of this referring to the vagus and glossopharyngeal nerves is given at p. 203. It should be noticed that there are only five strands indicated as springing from the spinal cord to form the vagus and glossopharyngeal nerves. It is however probable that there are even from the first a greater number of strands than this.

Fig. 2. Section through the hinder part of the medulla oblongata, stage between K and L. Zeiss A, ocul. 2.

It shews (1) The vagus commissure with branches on one side from the medulla. (2) The intestinal branch of the vagus giving off a nerve to the lateral line.

Fig. 3. Longitudinal and vertical section through the head of a Scyllium embryo of stage L. Zeiss a, ocul. 2.

It shews the course of the anterior branch of the seventh nerve (vii.); especially with relation to the ophthalmic branch of the fifth nerve (v. *o. th.*).

Fig. 4 *a* and 4 *b*. Two horizontal and longitudinal sections through the head of a Scyllium embryo belonging to stage O. Zeiss a, ocul. 2.

4 *a* is the most dorsal of the two sections, and shews the course of the anterior branch of the seventh nerve above the eye.

4 *b* is a slightly more ventral section, and shews the course of the fifth nerve.

Fig. 5. Longitudinal and horizontal section through the hind-brain at stage O, shewing the roots of the vagus and glossopharyngeal nerves in the brain. Zeiss B, ocul. 2.

There appears to be one root in the brain for the glossopharyngeal, and at least six for the vagus. The fibres from the roots divide in many cases into two bundles before leaving the brain. Swellings of the brain towards the interior of the fourth ventricle are in connection with the first five roots of the vagus, and the glossopharyngeal root; and a swelling is also intercalated between the first vagus root and the glossopharyngeal root.

Fig. 6. Horizontal section through a part of the choroid slit at stage P. Zeiss B, ocul. 2.

The figure shews (1) the rudimentary processus falciformis (*p. fal.*) giving origin to the vitreous humour; and (2) the hyaloid membrane (*hy. m.*) which is seen to adhere to the retina, and not to the vitreous humour or processus falciformis.

XV

Pl. XVII

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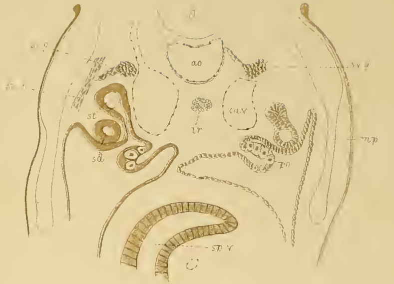

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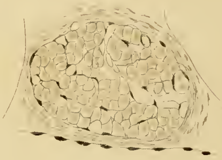

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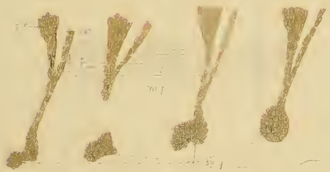

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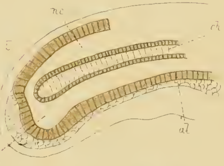

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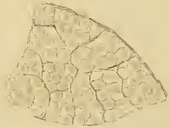

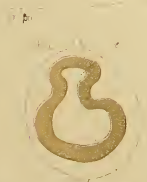

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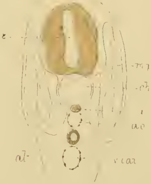

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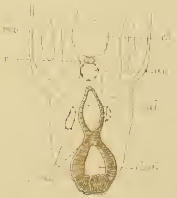

W. West & Co. lith.

EXPLANATION OF PLATE XVII.

Complete list of reference letters.

Nervous System.

sy. g. sympathetic ganglion. *sp. n.* spinal nerve.
p r. posterior root of spinal nerve. *a r.* anterior root of spinal nerve.
n. c. neural canal.

Alimentary Canal.

al. alimentary canal. *um. c.* umbilical canal.
hp. d. ductus choledochus. *du.* duodenum. *pan.* pancreas.
sp. v. intestine with rudiment of spiral valve. *s. œs.* solid œsophagus.
al. v. caudal vesicle of the postanal gut. *cl. al.* cloacal section of alimentary canal.

General.

mp. muscle-plate.
m p.l. muscle-plate sending a prolongation into the limb.
s t. segmental tube. *s d.* segmental duct. *ca. v.* cardinal vein.
v. cau. caudal vein. *ao.* dorsal aorta. *aur.* auricle of heart.
ch. notochord. *p o.* primitive ovum. *ir.* interrenal body.
pp. body-cavity. *ep. pp.* epithelial lining of the body-cavity.
me. mesentery. *t. s.* tail swelling. *x.* subnotochordal rod.

Fig. 1. Transverse section through the anterior abdominal region of an embryo of a stage between K and L. Zeiss B, ocul. 2. Reduced one-third.

The section illustrates the junction of a sympathetic ganglion with a spinal nerve and the sprouting of the muscle-plates into the limbs (*m p. l.*).

Fig. 2. Transverse section through the abdominal region of an embryo belonging to stage L. Zeiss B, ocul. 2. Reduced one-third.

The section illustrates the junction of a sympathetic ganglion with a spinal nerve, and also the commencing formation of a branch from the aorta (still solid) which will pass through the sympathetic ganglion, and forms the first sign of the conversion of part of a sympathetic ganglion into one of the suprarenal bodies.

Fig. 3. Longitudinal and vertical section of an embryo of a stage between L and M, shewing the successive junctions of the spinal nerves and sympathetic ganglia.

Fig. 4. Section through the solid œsophagus during stage L. Zeiss A, ocul. 1. The section is taken through the region of the heart, so that the cavity of the auricle (*aur*) lies immediately below the œsophagus.

Fig. 5. Optical section of the tail of an embryo between stages I and K, shewing the junction between the neural and alimentary canals.

Fig. 6. Four sections through the caudal region of an embryo belonging to stage K, shewing the condition of the postanal section of the alimentary tract. Zeiss A, ocul. 2. An explanation of these figures is given on p. 220.

Fig. 7. Section through the interrenal body of a Scyllium embryo belonging to stage Q. Zeiss C, ocul. 2.

Fig. 8. Portion of a section of the interrenal body of an adult Scyllium. Zeiss C, ocul. 2.

XV

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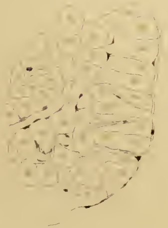

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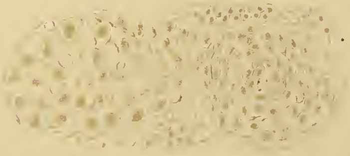

F.M.B. [illegible]

EXPLANATION OF PLATE XVIII.

Complete list of reference letters.

NERVOUS SYSTEM.

sp. n. spinal nerve. *sy. g.* sympathetic ganglion. *n.* nerve.

ALIMENTARY CANAL.

cl. cloaca. *in. cl.* cloacal involution. *œ. ep.* œsophageal epithelium. *th.* thyroid body. *pan.* pancreas.

GENERAL.

pp. body cavity. *ca. v.* cardinal vein. *cau. v.* caudal vein. *v. ao.* ventral aorta (anterior continuation of bulbus arteriosus). *aur.* auricle. *ven.* ventricle. *w. d.* Wolffian duct. *o. d.* oviduct. *u.* ureter. *ab. p.* abdominal pocket (pore). *p c.* pericardium. *m. m.* muscles. *s r.* suprarenal body. *ly.* lymphoid tissue.

Fig. 1 *a*, 1 *b*, 1 *c*. Three sections through the cloacal region of an embryo belonging to stage O. Fig. 1 *a* is the anterior of the three sections. Zeiss A, ocul. 2. Reduced one-third.

Fig. 1 *a* shews the cloacal involution at its deepest part abutting on the cloacal section of the alimentary tract.

Fig. 1 *b* is a section through a point somewhat behind this close to the opening of the Wolffian ducts into the cloaca.

Fig. 1 *c* shews the opening to the exterior in the posterior part of the cloaca, and also the rudiments of the two abdominal pockets (*ab. p.*).

Fig. 2. Section through the cloacal region of an embryo belonging to stage P. Zeiss A, ocul. 2.

The figure shews the solid anterior extremity of the cloacal involution.

Fig. 3. Longitudinal vertical section through the thyroid body in a stage between O and P. Zeiss *aa*, ocul. 1.

The figure shews the solid thyroid body (*th.*) connected in front with throat, and terminating below the bulbus arteriosus.

Fig. 4. Pancreas (*pan*) and adjoining part of the alimentary tract in longitudinal section, from an embryo between stages L and M. Zeiss A, ocul. 2.

Fig. 5. Portion of liver network of stage L. Zeiss. C ocul. 2. The section is intended to illustrate the fact that the tubules or cylinders of which the liver is composed are hollow and not solid. Between the liver tubules are seen blood spaces with distinct walls, and blood corpuscles in their interior.

Fig. 6. Section through part of one of the suprarenal bodies of an adult Scyllium hardened in chromic acid. Zeiss C, ocul. 2. The section shews the columnar cells forming the cortex and the more polygonal cells of the medulla.

Fig. 7. Transverse section through the anterior suprarenal body of an adult Scyllium. Zeiss B, ocul. 2. Reduced one-third. The tissue of the suprarenal body has not been filled in, but only the sympathetic ganglion cells which are seen to be irregularly scattered through the substance of the body. The entrance of the nerve (*n*) is shewn, and indications are given of the distribution of the nerve-fibres.

Fig. 8. Section through the sympathetic ganglion of a Scyllium embryo between stages M and N, shewing the connecting trunk between the suprarenal body and the spinal nerve (*sp. n.*), and the appearance of an indication in the ganglion of a portion more directly connected with the nerve. Zeiss D, ocul. 2.

Fig. 9. Section through one of the anterior sympathetic ganglia of an embryo of stage Q, shewing its division into a true ganglionic portion (*sy. g.*), and a suprarenal body (*s r*). Zeiss C, ocul. 2.

XIX.

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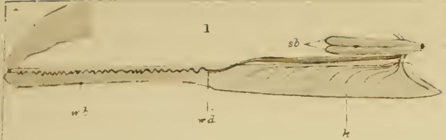

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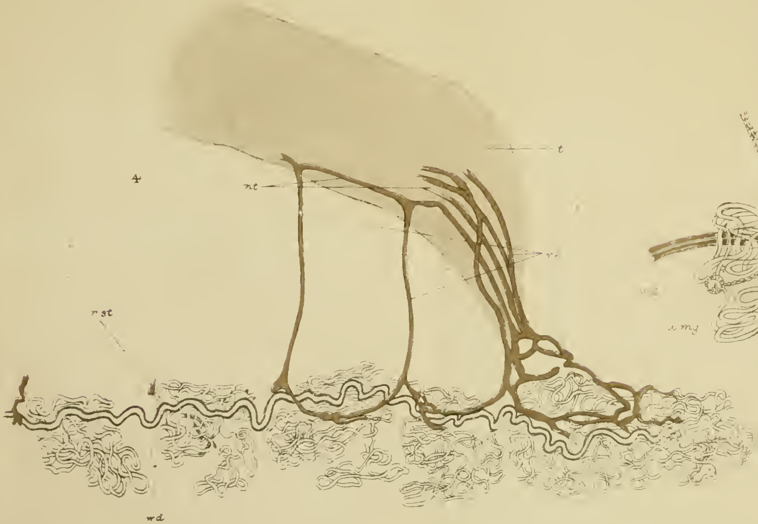

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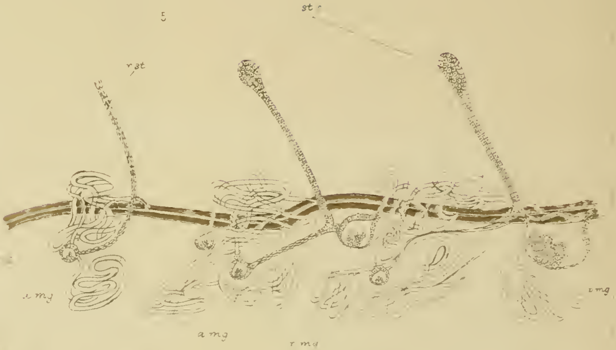

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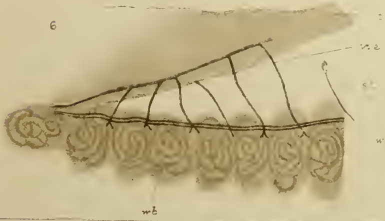

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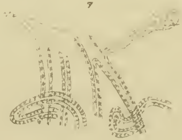

F. M. Balfour del.

EXPLANATION OF PLATE XIX.

Complete list of reference letters.

a.mg.	accessory Malpighian body.
k.	true kidney.
l.c.	longitudinal canal of the Wolffian body connected with vasa efferentia.
nt.	network and central canal at the base of the testis.
o.	external aperture of urinal cloaca.
o.u.	openings of ureters in Wolffian duct in the female (Fig. 3).
p.mg.	primary Malpighian body.
r.st.	rudimentary segmental tube.
s.b.	seminal bladder.
st.	segmental tube.
st.o.	opening of segmental tube into body-cavity.
t.	testis.
u.	ureters.
v.e.	vas efferens.
w.b.	Wolffian body.
w.d.	Wolffian duct.

Fig. 1. Diagrammatic representation of excretory organs on one side of a male Scyllium canicula, natural size.

Fig. 2. Diagrammatic representation of the kidney proper on one side of a female Scyllium canicula, natural size, shewing the ducts of the kidney and the dilated portion of the Wolffian duct.

Fig. 3. Opening of the ureters into the Wolffian duct of a female Scyllium canicula. The figure represents the Wolffian ducts (*w.d*) with ventral portion removed so as to expose their inner surface, and shews the junction of the two W. ducts to form the common urinal cloaca, the single external opening of this (*o*), and openings of ureters into one Wolffian duct (*ou*).

Fig. 4. Anterior extremity of Wolffian body of a young male Scyllium canicula shewing the vasa efferentia and their connection with the kidneys and the testis. The vasa efferentia and longitudinal canal are coloured to render them distinct. They are intended to be continuous with the uncoloured coils of the Wolffian body, though this connection has not been very successfully rendered by the artist.

Fig. 5. Part of the Wolffian body of a nearly ripe male embryo of Scyllium canicula as a transparent object. Zeiss a a, ocul. 3. The figure shews two segmental tubes opening into the body-cavity and connected with a primary Malpighian body, and also, by a fibrous connection, with a secondary Malpighian body of preceding segment. It also shews one segmental tube (*r.st*) imperfectly connected with the accessory Malpighian body of the preceding segment of the kidney. The coils of the kidney are represented somewhat diagrammatically.

Fig. 6. Vasa efferentia of a male embryo of Scyllium canicula eight centimetres in length. Zeiss a a, ocul. 2.

There are seen to be at the least six and possibly seven distinct vasa going to as many segments of the Wolffian body and connected with a longitudinal canal in the base of the testis. They were probably also connected with a longitudinal canal in the Wolffian body, but this could not be clearly made out.

Fig. 7. The anterior four vasa efferentia of a nearly ripe embryo. Connected with the foremost one is seen a body which looks like the remnant of a segmental tube and its opening (*r. st* ?).

Fig. 8. Testis and anterior part of Wolffian body of an embryo of Squatina vulgaris.

The figure is intended to illustrate the arrangement of the vasa efferentia. There are five of these connected with a longitudinal canal in the base of the testis, and with another longitudinal canal in the Wolffian body. From the second longitudinal canal there pass off four ducts to as many Malpighian bodies. Through the Malpighian bodies these ducts are continuous with the several coils of the Wolffian body, and so eventually with the Wolffian duct. Close to the hindermost vas efferens is seen a body which resembles a rudimentary segmental tube (*r. st.* ?).

X

Plate XX.

EXPLANATION OF PLATE XX.

Complete list of reference letters.

ca. v.	cardinal vein.
ge.	germinal epithelium.
mg.	Malpighian body.
od.	oviduct or Müllerian duct of the female.
od'.	Müllerian duct of the male.
px.	growth from vesicle at the end of a segmental tube to join the collecting tube of the preceding segment.
ru.	ureter commencing to be formed.
s. d.	segmental duct.
s. t.	segmental tube.
sur.	suprarenal body.
u.	ureter.
w.d.	Wolffian duct.

Fig. 1 A, 1 B, 1 C, 1 D. Four sections from a female Scyllium canicula of a stage between M and N through the part where the segmental duct becomes split into Wolffian duct and oviduct. Zeiss B, ocul. 2. Fig 1 A is the foremost section.

The sections shew that the oviduct arises as a thickening on the under surface of the segmental duct into which at the utmost a very narrow prolongation of the lumen of the segmental duct is carried. The small size of the lumen of the Wolffian duct in the foremost section is due to the section passing through nearly its anterior blind extremity.

Fig. 2. Section close to the junction of the Wolffian duct and oviduct in a female embryo of Scyllium canicula belonging to stage N. Zeiss B, ocul. 2.

The section represented shews that in some instances the formation of the oviduct and Wolffian duct is accompanied by a division of the lumen of the segmental duct into two not very unequal parts.

Fig. 3 A, 3 B, 3 C. Three sections illustrating the formation of a ureter in a female embryo belonging to stage N. Zeiss B, ocul. 2.

Fig. 3 A is the foremost section.

The figures shew that the lumen of the developing ureter is enclosed in front by an independent wall (Fig. 3 A), but that further back the lumen is partly shut in by the subjacent Wolffian duct, while behind no lumen is present, but the ureter ends as a solid knob of cells without an opening into the Wolffian duct.

Fig. 4. Section through the ureters of the same embryo as Fig. 3, but nearer the cloaca. Zeiss B, ocul. 2.

The figure shews the appearance of a transverse section through the wall of cells above the Wolffian duct formed by the overlapping ureters, the lumens of which appear as perforations in it. It should be compared with Fig. 9 A, which represents a longitudinal section through a similar wall of cells.

Fig. 5. Section through the ureters, the Wolffian duct and the oviduct of a female embryo of Scy. canicula belonging to stage P. Zeiss B, ocul. 2.

Fig. 6. Section of part of the Wolffian body of a male embryo of Scyllium canicula belonging to stage O. Zeiss B, ocul. 2.

The section illustrates (1) the formation of a Malpighian body (*mg*) from the dilatation at the end of a segmental tube, (2) the appearance of the rudiment of the Müllerian duct in the male (*od'*).

Figs. 7 *a*, 7 *b*. Two longitudinal and vertical sections through part of the kidney of an embryo between stages L and M. Zeiss B, ocul. 2.

7 *a* illustrates the parts of a single segment of the Wolffian body at this stage, vide p. 261. The segmental tube and opening are not in the plane of the section, but the dilated vesicle is shewn into which the segmental tube opens.

7 *b* is taken from the region of the kidney proper. To the right is seen the opening of a segmental tube into the body-cavity, and in the segment to the left the commencing formation of a ureter, vide p. 272.

Fig. 8. Longitudinal and vertical section through the posterior part of the kidney proper of an embryo of Scyllium canicula at a stage between N and O. Zeiss A, ocul. 2.

The section shews the nearly completed ureters, developing Malpighian bodies, &c.

Fig. 9. Longitudinal and vertical section through the anterior part of the kidney proper of the same embryo as Fig. 8. Zeiss A, ocul. 2.

The figure illustrates the mode of growth of the developing ureters.

9 A. More highly magnified portion of the same section as Fig. 9.

Compare with transverse section Fig. 4.

Fig. 10. Longitudinal and vertical section through part of the Wolffian body of an embryo of Scyllium canicula at a stage between O and P.

The section contains two examples of the budding out of the vesicle of a segmental tube to form a Malpighian body in its own segment and to unite with the tubulus of the preceding segment close to its opening into the Wolffian duct.

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