Cambridge – University

k

STUDIES

FROM THE

MORPHOLOGICAL LABORATORY

IN THE

UNIVERSITY OF CAMBRIDGE.

EDITED BY

F. M. BALFOUR, M.A., F.R.S., x ref
FELLOW OF TRINITY COLLEGE, CAMBRIDGE.

Vol. I. Parts I. II.

London:
C. J. CLAY AND SON,
CAMBRIDGE UNIVERSITY PRESS WAREHOUSE,
AVE MARIA LANE.
1884

CONTENTS OF PART I.

N.B.—The papers marked with *one asterisk* are reprinted from the 'Quarterly Journal of Microscopical Science,' those with *two asterisks*, are reprinted from the 'Proceedings of the Cambridge Philosophical Society.'

CONTENTS OF PART II.

N.B.—The papers marked with *one asterisk* are reprinted from the 'Quarterly Journal of Microscopical Science,' the papers with *two asterisks* are reprinted from the 'Proceedings of the Royal Society,' and the paper with *three asterisks* from the 'Proceedings of the Zoological Society.'

STUDIES

FROM THE

MORPHOLOGICAL LABORATORY

IN THE

UNIVERSITY OF CAMBRIDGE.

EDITED BY

F. M. BALFOUR, M.A., F.R.S.,
FELLOW OF TRINITY COLLEGE, CAMBRIDGE.

WILLIAMS AND NORGATE,
14, HENRIETTA STREET, COVENT GARDEN, LONDON;
AND 20, SOUTH FREDERICK STREET, EDINBURGH.
1880.

LONDON:
PRINTED BY J. E. ADLARD, BARTHOLOMEW CLOSE.

DEDICATED

TO

MICHAEL FOSTER.

CONTENTS.

N.B.—The papers marked with *one asterisk* are reprinted from the 'Quarterly Journal of Microscopical Science,' those with *two asterisks*, are reprinted from the 'Proceedings of the Cambridge Philosophical Society.'

On the EXISTENCE *of a* HEAD-KIDNEY *in the* EMBRYO CHICK, *and on* CERTAIN POINTS *in the* DEVELOPMENT *of the* MÜLLERIAN DUCT. By F. M. BALFOUR, M.A., Fellow of Trinity College, Cambridge; and ADAM SEDGWICK, B.A., Scholar of Trinity College, Cambridge. (With Plates I and II.)

THE following paper is divided into three sections. The first of these records the existence of certain structures in the embryo chick, which eventually become in part the abdominal opening of the Müllerian duct, and which, we believe, correspond with the head-kidney, or "Vorniere" of German authors. The second deals with the growth and development of the Müllerian duct. With reference to this we have come to the conclusion that the Müllerian duct does not develop entirely independently of the Wolffian duct. The third section of our paper is of a more general character, and contains a discussion of the rectifications in the views of the homologies of the parts of the excretory system in Aves, necessitated by the results of our investigations.

We have, as far as possible, avoided entering into the extended literature of the excretory system, since this has been very fully given in three general papers which have recently appeared by Semper,[1] Fürbinger,[2] and by one of us.[3]

All recent observers, including Braun[4] for Reptilia, and Egli[5] for Mammalia, have stated that the Müllerian duct develops as a groove in the peritoneal epithelium, which is continued backward as a primitively solid rod in the space between the Wolffian duct and peritoneal epithelium.

---

[1] "Das Urogenital System der Plagiostomen." 'Arbeiten a. d. Zool.-Zoot. Institut. Würzburg.'

[2] "Zur Vergl. Anat. u. Entwick. d. Excretionsorgane d. Vertebraten." 'Morphologisches Jahrbuch,' vol. iv.

[3] "On the Origin and History of the Urino-genital Organs of Vertebrates." 'Journal of Anat. and Phys.,' vol. x.

[4] 'Arbeiten a. d. zool.-zoot. Institut. Würzburg,' vol. iv.

[5] 'Beitr. zur Anat. u. Entwick. d. Geschlechtsorgane,' Inaug. Diss., Zurich, 1876.

In our preliminary account we stated,[1] in accordance with the general view, that the Müllerian duct was formed as a groove, or elongated involution of the peritoneal epithelium adjoining the Wolffian duct. We have now reason to believe that this is not the case. In the earliest condition of the Müllerian duct which we have been able to observe, it consists of three successive open involutions of the peritoneal epithelium, connected together by more or less well-defined ridge-like thickenings of the epithelium. We believe, on grounds hereafter to be stated, that the whole of this formation is equivalent to the head-kidney of the Icthyopsida. The head-kidney, as we shall continue to call it, takes its origin from the layer of thickened epithelium situated near the dorsal angle of the body cavity, close to the Wolffian duct, which has been known since the publication of Waldeyer's important researches as the germinal epithelium. The anterior of the three open involutions or grooves is situated some little distance behind the front end of the Wolffian duct. It is simply a shallow groove in the thickest part of the germinal epithelium, and forms a corresponding projection into the adjacent stroma. In front the projection is separated by a considerable interval from the Wolffian duct; but near its hindermost part it almost comes into contact with the Wolffian duct. The groove extends in all for about five of our sections, and then terminates by its walls becoming gradually continued into a slight ridge-like thickening of the germinal epithelium. The groove arises as a simple depression in a linear area of thickened germinal epithelium. The linear area is, however, continued very considerably further forward than the groove, and sometimes exhibits a slight central depression, which might be regarded as a forward continuation of the groove. The passage from the groove to the ridge may best be conceived by supposing the groove to be suddenly filled up, so as to form a solid ridge pointing inwards towards the Wolffian duct.

The ridge succeeding the first groove is continued for about six sections, and is considerably more prominent at its posterior extremity than in front. It is replaced by groove number two, which appears as if formed by the reverse process to that by which the ridge arose, viz., by a hollowing out of the ridge on the side towards the body cavity. The wall of the second groove is, after a few sections, continued into a second ridge or thickening of the germinal epithelium, which, however, is so faintly marked as to be hardly visible in its middle part. In its turn this ridge is replaced by the third and last groove. This vanishes after one or two sections, and behind the point of its disappearance we have failed to find any further traces of the

---

[1] 'Proceedings of Royal Society,' 1878.

head-kidney. The whole formation extends through about twenty-four of our sections and one and a half segments (muscle-plates).

We have represented (Plate I, series A, Nos. 1—10) a fairly complete series of sections through part of the head-kidney of an embryo slightly older than that last described, containing the second and third grooves and accessory parts. The connection between the grooves and the ridges is very well illustrated in Nos. 3, 4, and 5, of this series. In No. 3 we have a prominent ridge, in the interior of which there appears in No. 4 a groove, which becomes gradually wider in Nos. 5 and 6. Both the grooves and ridges are better marked in this than in the younger stage; but the chief difference between the two stages consists in the third groove no longer forming the hindermost limit of the head-kidney. Instead of this, the last groove (No. 7) terminates by the upper part of its walls becoming constricted off as a separate rod, which appears at first to contain a lumen continuous with the open groove. This rod (Nos. 7, 8, 9, 10) situated between the germinal epithelium and Wolffian duct is continued backward for some sections. It finally terminates by a pointed extremity, composed of not more than two cells abreast (Nos. 8—10).

Our third stage, sections of which are represented in series B (Plate I), is considerably advanced beyond that last described. The most important change which has been effected concerns the ridges connecting the successive grooves. A lumen has appeared in each of these, which seems to open at both ends into the adjacent grooves. At the same time the cells, which previously constituted the ridge, have become (except where they are continuous with the walls of the grooves) partially constricted off from the germinal epithelium. The ridges, in fact, now form ducts situated in the stroma of the ovarian ridge, in the space between the Wolffian duct and the germinal epithelium. The duct continuous with the last groove is somewhat longer than before. In a general way, the head-kidney may now be described as a duct opening into the body cavity by three groove-like apertures, and continuous behind with the rudiment of the true Müllerian duct. Although the general constitution of the head-kidney at this stage is fairly simple, there are a few features in our sections which we do not fully understand, and a few points about the organ which deserve a rather fuller description than we have given in this general sketch.

The anterior groove (No. 1—3, series B, Pl. I) is at first somewhat separated from the Wolffian duct, but approaches close to it in No. 3. In Nos. 2 and 3 there appears a rod-like body on the outer side of the walls of the groove. In No. 2

this body is disconnected with the walls of the groove, and even appears as if formed by a second invagination of the germinal epithelium. In No. 3 this body becomes partially continuous with the walls of the groove, and finally in No. 4 it becomes completely continuous with the walls of the groove, and its lumen communicates freely with the groove.[1]

The last trace of this body is seen on the upper wall of the groove in No. 5. We believe that the body (r_1) represents the ridge between the first and second grooves of the earlier stage; so that in passing from No. 3 to No. 5 we pass from the first to the second groove. The meaning of the features of the body (r_1) in No. 2 we do not fully understand, but cannot regard them as purely accidental, since we have met with more or less similar features in other series of sections. The second groove becomes gradually narrower, and finally is continued into the second ridge (No. 8). The ridge contains a lumen, and is only connected with the germinal epithelium by a narrow wall of cells. A narrow passage from the body cavity leads into that wall for a short distance in No. 8, but it is probably merely the hinder end of the groove of No. 7. The third groove appears in No. 11, and opens into the lumen of the second ridge (r_2) in No. 12. In No. 13 the groove is closed, and there is present in its place a duct (r_3) connected with the germinal epithelium by a wall of cells. This duct is the further development of the third ridge of the last stage; its lumen opens into the body cavity through the third and last groove (gr_3). In the next section this duct (r_3) is entirely separated from the germinal epithelium, and it may be traced backwards through several sections until it terminates by a solid point, very much as in the last stage.

In the figures of this series (B) there may be noticed on the outer side of the Müllerian duct a fold of the germinal epithelium (x) forming a second groove. It is especially conspicuous in the first six sections of the series. This fold sometimes becomes much deeper, and then forms a groove, the upper end of which is close to the grooves of the head-kidney. It is very often much deeper than these are, and without careful study might easily be mistaken for one of these grooves. Fig. C, taken from a series slightly younger than B, shows this groove (x) in its most exaggerated form.

The stage we have just described is that of the fullest development of the head-kidney. In it, as in all the previous stages, there appear to be only three main openings into the body-cavity; but we have met in some of our sections with indications of the possible presence of one or two extra rudimentary grooves.

---

[1] A deep focus of the rather thick section represented in No. 3 showed the body much more nearly in the position it occupies in No. 4.

In an embryo not very much older than the one last described the atrophy of the head-kidney is nearly completed, and there is present but a single groove opening into the body cavity.

In series D (Pl. II) are represented a number of sections from an embryo at this stage. Nos. 1 and 2 are sections through the hind end of the single groove now present. Its walls are widely separated from the Wolffian duct in front, but approach close to it at the hinder termination of the groove (No. 2). The features of the single groove present at this stage agree closely with those of the anterior groove of the previous stages. The groove is continued into a duct—the Müllerian duct (as it may now be called, but in a previous stage the hollow ridge connecting the first and second grooves of the head kidney)—which, after becoming nearly separated from the germinal epithelium, is again connected to it by a mass of cells at two points (Nos. 5, 6, and 8). The germinal epithelium is slightly grooved and is much reduced in thickness at these points of contact (gr_2 and gr_3), and we believe that they are the remnants of the posterior grooves of the head-kidney present at an earlier stage.

The Müllerian duct has by this stage grown much further backwards, but the peculiarities of this part of it are treated in a subsequent section.

We consider that, taking into account the rudiments we have just described, as well as the fact that the features of the single groove at this stage correspond with those of the anterior groove at an earlier stage, we are fully justified in concluding that *the permanent abdominal opening of the Müllerian duct corresponds with the anterior of our three grooves.*

Although we have, on account of their indefiniteness, avoided giving the ages of the chicks in which the successive changes of the head-kidney may be observed, we may, perhaps, state that all the changes we have described are usually completed between the 90th and 120th hour of incubation.

The Glomerulus of the Head-Kidney.

In connection with the head-kidney in Amphibians there is present, as is well known, a peculiar vascular body usually described as the glomerulus of the head-kidney. We have found in the chick a body so completely answering to this glomerulus that we have hardly any hesitation in identifying it as such.

In the chick the glomerulus is paired, and consists of a vascular outgrowth or ridge projecting into the body cavity on each side at the root of the mesentery. It extends from the anterior end of the Wolffian body to the point where the foremost opening of the head-kidney commences. We have found it at a period slightly earlier than that of the first development of the head-kidney. It is represented in figs. E and F, Pl. II *gl,* and is seen to form a somewhat irregular projection into the body cavity, covered by a continuation of the peritoneal epithelium, and attached by a narrow stalk to the insertion of the embryonic mesentery (*me*).

In the interior of this body is seen a stroma with numerous vascular channels and blood-corpuscles, and a vascular connection is apparently becoming established, if it is not so already, between the glomerulus and the aorta. We have reason to think that the corpuscles and vascular channels in the glomerulus are developed *in situ.* The stalk connecting the glomerulus with the attachment of the mesentery varies in thickness in different sections, but we believe that the glomerulus is continued unbroken throughout the very considerable region through which it extends. This point is, however, difficult to make sure of owing to the facility with which the glomerulus breaks away.

At the stage we are describing, no true Malpighian bodies are present in the part of the Wolffian body on the same level with the anterior end of the glomerulus, but the Wolffian body merely consists of the Wolffian duct. At the level of the posterior part of the glomerulus this is no longer the case, but here a regular series of primary Malpighian bodies is present (using the term "primary" to denote the Malpighian bodies developed directly out of part of the primary segmental tubes), and the glomerulus of the head-kidney may frequently be seen in the same section as a Malpighian body. In most sections the two bodies appear quite disconnected, but in those sections in which the *glomerulus* of the Malpighian body comes into view it is seen to be derived from the same formation as the glomerulus of the head-kidney (Plate II, fig. F). It would seem, in fact, that the vascular tissue of the glomerulus of the head-kidney grows into the concavity of the Malpighian bodies. Owing to the stage we are now describing, in which we have found the glomerulus most fully developed, being prior to that in which the head-kidney appears, it is not possible to determine with certainty the position of the glomerulus in relation to the head-kidney. After the development of the head-kidney it is found, however, as we have already stated, that the glomerulus terminates at a point just in front of the anterior opening of the head-kidney. It is less developed than before, but is still present up to the period of the atrophy of the head-kidney. It does not apparently alter in constitution, and we have not thought it worth while giving any further representations of it during the later stages of its existence.

Summary of the development of the head-kidney and glomerulus.—The first rudiment of the head-kidney arises as three successive grooves in the thickened germinal epithelium, connected by ridges and situated some way behind the front end of the Wolffian duct. In the next stage the three ridges connecting the grooves have become more marked, and in each of them a lumen has appeared, opening at both extremities into the adjoining grooves. Still later the ridges become more or less completely detached from the peritoneal epithelium, and the whole head-kidney then consists of a slightly convoluted duct, with, at the least, three peritoneal openings, which is posteriorly continued into the Müllerian duct. Still later the head-kidney atrophies, its two posterior openings vanishing, and its anterior opening remaining as the permanent opening of the Müllerian duct. The glomerulus arises as a vascular prominence at the root of the mesentery, slightly prior in point of time to the head-kidney, and slightly more forward than it in position. We have not traced its atrophy.

We stated in our preliminary paper that the peculiar structures we had interpreted as the head-kidney had completely escaped the attention of previous observers, though we called attention to a well-known figure of Waldeyer's (copied in the 'Elements of Embryology,' fig. 51). In this figure a connection between the germinal epithelium and the Müllerian duct is drawn, which is probably part of the head-kidney, and may be compared with our figures (Series B, No. 8, and Series D, No. 4). Since we made the above statement, Dr. Gasser has called our attention to a passage in his valuable memoir on 'The Development of the Allantois,'[1] in which certain structures are described which are, perhaps, identical with our head-kidney. The following is a translation of the passage:

"In the upper region of Müller's duct I have often observed small canals, especially in the later stages of development, which appear as a kind of doubling of the duct, and run for a short distance close to Müller's duct and in the same direction, opening, however, into the body cavity posterior to the main duct. Further, one may often observe diverticula from the extreme anterior end of the oviduct of the bird, which form blind pouches and give one the impression of being receptacula seminis. Both these appearances can quite well be accounted for on the supposition that an abnormal communication is effected between the germinal epithelium and Müller's duct at unusual places; or else that an attempt at such a communication is made, resulting, however, only in the formation of a diverticulum of the wall of the oviduct."

The statement that these accessory canals are late in developing, prevents us from feeling quite confident that they really correspond with our head-kidney.

---

[1] 'Beiträge zur Entwicklungsgeschichte d. Allantois der Müller'schen Gänge u. des Afters.' Frankfurt, 1874.

Before passing on to the other parts of this paper it is necessary to say a few words in justification of the comparison we have made between the modified abdominal extremity of the Müllerian duct in the chick and the head-kidney of the Icthyopsida.

For the fullest statement of what is known with reference to the anatomy and development of the head-kidney in the lower types we may refer to Spengel and Fürbringer.[1] We propose ourselves merely giving a sufficient account of the head-kidney in Amphibia (which appears to be the type in which the head-kidney can be most advantageously compared with that in the bird) to bring out the grounds for our determination of the homologies.

The development of the head-kidney in Amphibia has been fully elucidated by the researches of W. Müller,[2] Götte,[3] and Fürbringer,[4] while to the latter we are indebted for a knowledge of the development of the Müllerian duct in Amphibians. The first part of the urino-genital system to develop is the segmental duct (Vornieregang of Fürbringer), which is formed by a groove-like invagination of the peritoneal epithelium. It becomes constricted into a duct first of all in the middle, but soon in the posterior part also. It then forms a duct, ending in front by a groove in free communication with the body cavity, and terminating blindly behind. The open groove in front at first deepens, and then becomes partially constricted into a duct, which elongates and becomes convoluted, but remains in communication with the body cavity by from two to four (according to the species) separate openings. The manner in which the primitive single opening is related to the secondary openings is not fully understood. By these changes there is formed out of the primitive groove an anterior glandular body, communicating with the body cavity by several apertures, and a posterior duct, which carries off the secretion of the gland, and which, though blind at first, eventually opens into the cloaca. In addition to these parts there is also formed on each side of the mesentery, opposite the peritoneal openings, a very vascular projection into this part of the body cavity, which is known as the glomerulus of the head-kidney, and which very closely resembles in structure and position the body to which we have assigned the same name in the chick.

The primitive segmental duct is at first only the duct for the head-kidney, but on the formation of the posterior parts of the kidney (Wolffian body, &c.) it becomes the duct for these also.

---

[1] Loc. cit.

[2] 'Jenaische Zeitschrift,' vol. ix, 1875.

[3] 'Entwickelungsgeschichte d. Unke.'

[4] Loc. cit.

After the Wolffian bodies have attained to a considerable development, the head-kidney undergoes atrophy, and its peritoneal openings become successively closed from before backwards. At this period the formation of the Müllerian duct takes place. It is a solid constriction of the ventral or lateral wall of the segmental duct, which subsequently becomes hollow, and acquires an opening into the body cavity *quite independent of the openings of the head-kidney.*

The similarity in development and structure between the head-kidney in Amphibia and the body we have identified as such in Aves, is to our minds too striking to be denied. Both consist of two parts—(1) a somewhat convoluted longitudinal canal, with a certain number of peritoneal openings; (2) a vascular prominence at the root of the mesentery, which forms a glomerulus. As to the identity in position of the two organs we hope to deal with that more fully in speaking of the general structure of the excretory system, but may say that one of us[1] has already, on other grounds, attempted to show that the abdominal opening of the Müllerian duct in the bird is the homologue of the abdominal opening of the segmental duct in Amphibia, Elasmobranchii, &c., and that we believe that this homology will be admitted by most anatomists. If this homology is admitted, the identity in position of this organ in Aves and Amphibia necessarily follows. The most striking difference between Aves and Amphibia in relation to these structures is the fact that in Aves the anterior pore of the head-kidney remains as the permanent opening of the Müllerian duct, while in Amphibia, the pores of the head-kidney atrophy, and an entirely fresh abdominal opening is formed for the Müllerian duct.

II.

The Growth of the Müllerian Duct.

Although a great variety of views have been expressed by different observers on the growth of the Müllerian duct, it is now fairly generally admitted that it grows in the space between a portion of the thickened germinal epithelium and the Wolffian duct, but quite independently of both of them. Both Braun and Egli, who have specially directed their attention to this point, have for Reptilia and Mammalia fully confirmed the views of previous observers. We were, nevertheless, induced, partly on account of the *à priori* difficulties of this view, and partly by certain peculiar appearances which we observed, to undertake

---

[1] Balfour, "Origin and History of Urinogenital Organs of Vertebrates." 'Journal of Anat. and Phys.,' vol. x, and "Monograph on Elasmobranch Fishes."

the re-examination of this point, and have found ourselves unable altogether to accept the general account. We propose first describing, in as matter-of-fact a way as possible, the actual observations we have made, and then stating what conclusions we think may be drawn from these observations.

We have found it necessary to distinguish three stages in the growth of the Müllerian duct. Our first stage embraces the period prior to the disappearance of the head-kidney. At this stage, the structure we have already spoken of as the rudiment of the Müllerian duct consists of a solid rod of cells, continuous with the third groove of the head-kidney. It extends through a very few sections, and terminates by a fine point of about two cells, wedged in between the Wolffian duct and germinal epithelium (described above, No. 7—10, series A, Plate I).

In an embryo slightly older than the above, such as that from which series B was taken, but still belonging to our first stage, a definite lumen appears in the anterior part of the Müllerian duct, which vanishes after a few sections. The duct terminates in a point which lies in a concavity of the wall of the Wolffian duct (Plate I, Nos. 1 and 2, series G). The limits of the Wolffian wall and the pointed termination of the Müllerian duct are in many instances quite distinct; but the outline of the Wolffian duct appears to be carried round the Müllerian duct, and in some instances the terminal point of the Müllerian duct seems almost to form an integral part of the wall of the Wolffian duct.

The second of our stages corresponds with that in which the atrophy of the head-kidney is nearly complete (series D and H, Plate II).

The Müllerian duct has by this stage made a very marked progress in its growth towards the cloaca, and, in contradistinction to the earlier stage, a lumen is now continued close up to the terminal point of the duct. In the two or three sections before it ends it appears as a distinct oval mass of cells (No. 10, series D, and No. 1, series H), without a lumen, lying between and touching the external wall of the Wolffian duct on the one hand, and the germinal epithelium on the other. It may either lie on the ventral side of the Wolffian duct (series D), or on the outer side (series H), but in either case is opposite the maximum thickening of that part of the germinal epithelium which always accompanies the Müllerian duct in its backward growth.

In the last section in which any trace of the Müllerian duct can be made out (series D, No. 11, and series H, No. 2), it has no longer an oval, well-defined contour, but appears to have completely fused with the wall of the Wolffian duct, which is accordingly very thick, and occupies the space which in the previous section was filled by its own wall and the Müllerian duct. In the following section the thickening in the wall of the Wolffian duct has disappeared (Plate II, series H, No. 3), and every trace of the Müllerian duct has vanished from view. The Wolffian duct is on one side in contact with the germinal epithelium.

The stage during which the condition above described lasts is not of long duration, but is soon succeeded by our third stage, in which a fresh mode of termination of the Müllerian duct is found. (Plate II, series I). This last stage remains up to about the close of the sixth day, beyond which our investigations do not extend.

A typical series of sections through the terminal part of the Müllerian duct at this stage presents the following features:

A few sections before its termination the Müllerian duct appears as a well-defined oval duct lying in contact with the wall of the Wolffian duct on the one hand and the germinal epithelium on the other (series I, No. 1). Gradually, however, as we pass backwards, the Müllerian duct dilates; the external wall of the Wolffian duct adjoining it becomes greatly thickened and pushed in in its middle part, so as almost to touch the opposite wall of the duct, and so form a bay in which the Müllerian duct lies (Plate II, series I, Nos. 2 and 3). As soon as the Müllerian duct has come to lie in this bay its walls lose their previous distinctness of outline, and the cells composing them assume a curious vacuolated appearance. No well-defined line of separation can any longer be traced between the walls of the Wolffian duct and those of the Müllerian, but between the two is a narrow clear space traversed by an irregular network of fibres, in some of the meshes of which nuclei are present.

The Müllerian duct may be traced in this condition for a considerable number of sections, the peculiar features above described becoming more and more marked as its termination is approached. It continues to dilate and attains a maximum size in the section or so before it disappears. A lumen may be observed in it up to its very end, but is usually irregular in outline and frequently traversed by strands of protoplasm. The Müllerian duct finally terminates quite suddenly (Plate II, series I, No. 4), and in the section immediately behind its termination the Wolffian duct assumes its normal appearance, and the part of its outer wall on the level of the Müllerian duct comes into contact with the germinal epithelium (Plate II, series I, No. 5).

We have traced the growing point of the Müllerian duct with the above features till not far from the cloaca, but we have not followed the last phases of its growth and its final opening into the cloaca.

In some of our embryos we have noticed certain rather peculiar structures, an example of which is represented at *y* in fig. K, taken from an embryo of 123 hours, in which all traces of the head-kidney had disappeared. It consists of a cord of cells, connecting the Wolffian duct and the hind end of the abdominal opening of the Müllerian duct. At the least one similar cord was met with in the same embryo, situated just behind the abdominal opening of the Müllerian duct. We have found similar structures in other embryos of about the same age, though never so well marked as in the embryo from which fig. K is taken. We have quite failed to make out the meaning, if any, of them.

Our interpretation of the appearances we have described in connection with the growth of the Müllerian duct can be stated in a very few words. Our second stage, where the solid point of the Müllerian duct terminates by fusing with the walls of the Wolffian duct, we interpret as meaning that the Müllerian is growing backwards as a solid rod of cells, split off from the outer wall of the Wolffian duct; in the same manner, in fact, as in Amphibia and Elasmobranchii. The condition of the terminal part of the Müllerian duct during our third stage cannot, we think, be interpreted in the same way, but the peculiarities of the cells of both Müllerian and Wolffian ducts, and the indistinctness of the outlines between them, appear to indicate that the Müllerian duct grows by cells passing from the Wolffian duct to it. In fact, although in a certain sense the growth of the two ducts is independent, yet the actual cells which assist in the growth of the Müllerian duct are, we believe, derived from the walls of the Wolffian duct.

III.

General Considerations.

The excretory system of a typical Vertebrate consists of the following parts:

1. A head-kidney with the characters already described.
2. A duct for the head-kidney—the segmental duct.
3. A posterior kidney—(Wolffian body, permanent kidney, &c. The nature and relation of these parts we leave out of consideration, as they have no bearing upon our present investigations.) The primitive duct for the Wolffian body is the segmental duct.
4. The segmental duct may become split into (*a*) a dorsal or inner duct, which serves as ureter (in the widest sense of the word); and (*b*) a ventral or outer duct, which has an opening

into the body cavity, and serves as the generative duct for the female, or for both sexes.

These parts exhibit considerable variations both in their structure and development, into some of which it is necessary for us to enter.

The head-kidney[1] attains to its highest development in the Marsipobranchii (Myxine, Bdellostoma). It consists of a longitudinal canal, from the ventral side of which numerous tubules pass. These tubules, after considerable subdivision, open by a large number of apertures into the pericardial cavity. From the longitudinal canal a few dorsal diverticula, provided with glomeruli, are given off. In the young the longitudinal canal is continued into the segmental duct; but this connection becomes lost in the adult. The head-kidney remains, however, through life. In Teleostei and Ganoidei (?) the head-kidney is generally believed to remain through life, as the dilated cephalic portion of the kidneys when such is present. In Petromyzon and Amphibia the head-kidney atrophies. In Elasmobranchii the head-kidney, so far as is known, is absent.

The development of the segmental duct and head-kidney (when present) is still more important for our purpose than their adult structure.

In Myxine the development of these structures is not known. In Amphibia and Teleostei it takes place upon the same type, viz., by the conversion of a groove-like invagination of the peritoneal epithelium into a canal open in front. The head-kidney is developed from the anterior end of this canal, the opening of which remains in Teleostei single and closes early in embryonic life, but becomes in Amphibia divided into two, three, or four openings. In Elasmobranchii the development is very different. "The first trace of the urinary system makes its appearance as a knob springing from the intermediate cell-mass opposite the fifth proto-vertebra. 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. The knob projects

---

[1] I am inclined to give up the view I formerly expressed with reference to the head-kidney and segmental duct, viz. "that they were to be regarded as the most anterior segmental tube, the peritoneal opening of which had become divided, and which had become prolonged backwards so as to serve as the duct for the posterior segmental tubes," and *provisionally* to accept the Gegenbaur-Fürbringer view which has been fully worked out and ably argued for by Fürbringer (loc. cit. p. 96). According to this view the head-kidney and its duct are to be looked on as the primitive and unsegmented part of the excretory system, more or less similar to the excretory system of many Trematodes and unsegmented Vermes. The segmental tubes I regard as a truly segmental part of the excretory system acquired subsequently.—F. M. B.

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."[1]

The difference in the development of the segmental duct in the two types (Amphibia and Elasmobranchii) is very important. In the one case a continuous groove of the peritoneal epithelium becomes constricted into a canal, in the other a solid knob of cells is continued into a rod, at first solid, which grows backwards without any apparent relation to the peritoneal epithelium.

The abdominal aperture of the segmental duct in Elasmobranchii, in that it becomes the permanent abdominal opening of the oviduct, corresponds physiologically rather with the abdominal opening of the Müllerian duct than with that of the segmental duct of Amphibia, which, after becoming divided up to form the pores of the head-kidney, undergoes atrophy. Morphologically, however, it appears to correspond with the opening of the segmental duct in Amphibia. We shall allude to this point more than once again, and give our grounds for the above view on p. 19.

The development of the segmental duct in Elasmobranchii as a solid rod is, we hope to show, of special importance for the elucidation of the excretory system of Aves.

The development of these parts Petromyzon is not fully known, but from W. Müller's account ('Jenaische Zeitschrift,' 1875) it would seem that an anterior invagination of the peri-

---

[1] In a note on p. 50 of his memoir Fürbringer criticises my description of the mode of growth of the segmental duct. The following is a free translation of what he says: "In Balfour's, as in other descriptions, an account is given of a backward growth, which easily leads to the supposition of a structure formed anteriorly forcing its way through the tissues behind. This is, however, not the case, since, to my knowledge, no author has ever detected a sharp boundary between the growing point of the segmental duct (or Müllerian duct) and the surrounding tissues." He goes on to say that "the growth in these cases really takes place by a differentiation of tissue along a line in the region of the peritoneal cavity." Although I fully admit that it would be far easier to homologise the development of the segmental duct in Amphibia and Elasmobranchii according to this view, I must nevertheless vindicate the accuracy of my original account. I have looked over my specimens again, since the appearance of Dr. Fürbringer's paper, and can find no evidence of the end of the duct becoming continuous with the adjoining mesoblastic tissues. In the section, before its disappearance, the segmental duct may, so far as I can make out, be seen as a very small but distinct rod, which is much more closely connected with the epiblast than with any other layer. From Gasser's observations on the Wolffian duct in the bird, I am led to conclude that it behaves in the same way as the segmental duct in the Elasmobranchii. I will not deny that it is possible that the growth of the duct takes place by wandering cells, but on this point I have no evidence, and must therefore leave the question an open one.—F. M. B.

toneal epithelium is continued backwards as a duct (segmental duct), and that the anterior opening subsequently becomes divided up into the various apertures of the head-kidney. If this account is correct, Petromyzon presents a type intermediate between Amphibia and Elasmobranchii. In certain types, viz. Marsipobranchii and Teleostei, the segmental duct becomes the duct for the posterior kidney (segmental tubes), but otherwise undergoes no further differentiation. In the majority of types, however, the case is different. In Amphibia,[1] as has already been mentioned, a solid rod of cells is split off from its ventral wall, which afterwards becomes hollow, acquires an opening into the body cavity, and forms the Müllerian duct.

In Elasmobranchii the segmental duct undergoes a more or less similar division. "It becomes longitudinally split into two complete ducts in the female, and one complete duct and parts of a second in the male. The resulting ducts are 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. 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."

It will be seen from the above that the Müllerian duct consists of two distinct parts—an anterior part with the abdominal opening, and a posterior part split off from the segmental duct. This double constitution of the Müllerian duct is of great importance for a proper understanding of what takes place in the Bird.

The Müllerian duct appears, therefore, to develop in nearly the same manner in the Amphibian and Elasmobranch type as a solid or nearly solid rod split off from the ventral wall of the segmental duct. But there is one important difference concerning the abdominal opening of the duct. In Amphibia this is a new formation, but in Elasmobranchii it is the original opening of the segmental duct. Although we admit that in a large number of points, including the presence of a head-kidney, the

---

[1] Fürbringer, loc. cit.

urino-genital organs of Amphibia are formed on a lower type than those of the Elasmobranchii, yet it appears to us that this does not hold good for the development of the Müllerian duct.

The above description will, we trust, be sufficient to render clear our views upon the development of the excretory system in Aves.

In the bird the excretory system consists of the following parts (using the ordinary nomenclature) which are developed in the order below.

1. Wolffian duct. 2. Wolffian body. 3. Head-kidney. 4. Müllerian duct. 5. Permanent kidney and ureter.

About 2 and 5 we shall have nothing to say in the sequel.

We have already in the early part of the paper given an account of the head-kidney and Müllerian duct, but it will be necessary for us to say a few words about the development of the Wolffian duct (so called). Without entering into the somewhat extended literature on the subject, we may state that we consider that the recent paper of Dr. Gasser[1] supplies us with the best extant account of the development of the Wolffian duct.

The first trace of it which he finds is visible in an embryo with eight proto-vertebræ as a slight projection from the intermediate cell mass towards the epiblast in the region of the three hindermost proto-vertebræ. In the next stage, with eleven proto-vertebræ, the solid rudiment of the duct extends from the fifth to the eleventh proto-vertebra, from the eighth to the eleventh proto-vertebra it lies between the epiblast and mesoblast, and is quite distinct from both, and Dr. Gasser distinctly states that in its growth backwards from the eighth proto-vertebra the Wolffian duct never comes into continuity with the adjacent layers.

In the region of the fifth proto-vertebra, where the duct was originally continuous with the mesoblast, it has now become free, but is still attached in the region of the sixth and to the eighth proto-vertebra. In an embryo with fourteen proto-vertebræ the duct extends from the fourth to the fourteenth proto-vertebra, and is now free between epiblast and mesoblast for its whole extent. It is still for the most part solid, though perhaps a small lumen is present in its middle part. In the succeeding stages the lumen of the duct gradually extends backwards and forwards, the duct itself also passes inwards till it acquires its final position close to the peritoneal epithelium; at the same time its hind end elongates till it comes into connection with the cloacal section of the hind-gut. It should be noted that the duct in its backward growth does not appear to come into continuity with the subjacent mesoblast, but behaves in this respect exactly as does the segmental duct in Elasmobranchii (*vide* note on p. 14).

---

[1] 'Arch. für Mic. Anat.,' vol. xiv.

The question which we propose to ourselves is the following:—What are the homologies of the parts of the Avian urinogenital system above enumerated? The Wolffian duct appears to us morphologically to correspond *in part* to the segmental duct,[1] or what Fürbringer would call the duct of the head-kidney. This may seem a paradox, since in birds it never comes into relation with the head-kidney. Nevertheless, we consider that this homology is morphologically established, for the following reasons:—

(1) That the Wolffian duct gives rise (*vide supra*, p. 12) to the Müllerian duct as well as to the duct of the Wolffian body. In this respect it behaves precisely as does the segmental duct of Elasmobranchii and Amphibia. That it serves as the duct for the Wolffian body, before the Müllerian duct originates from it, is also in accordance with what takes place in other types.

(2) That it develops in a strikingly similar manner to the segmental duct of Elasmobranchii.

We stated expressly that the Wolffian duct corresponded only in part to the segmental duct. It does not, in fact, in our opinion, correspond to the whole segmental duct, but to the segmental duct minus the anterior abdominal opening in Elasmobranchii, which becomes the head-kidney in other types. In fact, we suppose that the segmental duct and head-kidney, which in the Ichthyopsida develop as a single formation, develop in the Bird as two distinct structures—one of these known as the Wolffian duct, and the other the head-kidney. If our view about the head-kidney is accepted the above position will hardly require to be disputed, but we may point out that the only feature in which the Wolffian duct of the Bird differs in development from the segmental duct of Elasmobranchii is in the absence of the knob, which forms the commencement of the segmental duct, and in which the abdominal opening is formed; so that the comparison of the development of the duct in the two types confirms the view arrived at from other considerations.

The head-kidney and Müllerian duct in the Bird must be considered together. The parts which they eventually give rise to after the atrophy of the head-kidney have almost universally been regarded as equivalent to the Müllerian duct of the Ichthyopsida. By Braun,[2] however, who from his researches on the lizard satisfied

---

[1] The views here expressed about the Wolffian duct are nearly though not exactly those which one of us previously put forward ('Urinogenital Organs of Vertebrates,' &c., p. 45-46), and with which Fürbringer appears exactly to agree. Possibly Dr. Fürbinger would alter his view on this point were he to accept the facts we believe ourselves to have discovered. Semper's view also differs from ours, in that he believes the Wolffian duct to correspond in its entirety with the segmental duct.

[2] "Urogenital System d. Reptilien." 'Arb. aus d. zool.-zoot. Inst.' Würzburg, vol. iv.

himself of the entire independence of the Müllerian and Wolffian ducts in the Amniota, the Müllerian duct of these forms is regarded as a completely new structure with no genetic relations to the Müllerian duct of the Ichthyopsida. Semper[1], on the other hand, though he accepts the homology of the Müllerian duct in the Ichthyopsida and Amniota, is of opinion that the anterior part of the Müllerian duct in the Amniota is really derived from the Wolffian duct, though he apparently admits the independent growth of the posterior part of the Müllerian duct. We have been led by our observations, as well as by our theoretical deductions, to adopt a view exactly the reverse of that of Professor Semper. We believe that the anterior part of the Müllerian duct of Aves, which is at first the head-kidney, and subsequently becomes the abdominal opening of the duct, is developed from the peritoneal epithelium independently of all other parts of the excretory system; but that the posterior part of the duct is more or less completely derived from the walls of the Wolffian duct. This view is clearly in accordance with our account of the facts of development in Aves, and it fits in very well with the development of the Müllerian duct in Elasmobranchii. We have already pointed out that in Elasmobranchii the Müllerian duct is formed of two factors—(1) of the whole anterior extremity of the segmental duct, including its abdominal opening; (2) of a rod split off from the ventral side of the segmental duct. In Birds the anterior part (corresponding to factor No. 1) of the Müllerian duct has a different origin from the remainder; so that if the development of the posterior part of the duct (factor No. 2) were to proceed in the same manner in Birds and Elasmobranchii, it ought to be formed at the expense of the Wolffian (*i. e.* segmental) duct, though in connection anteriorly with the head-kidney. And this is what actually appears to take place.

So far the homologies of the avian excretory system are fairly clear; but there are still some points which have to be dealt with in connection with the permanent opening of the Müllerian duct, and the relatively posterior position of the head-kidney. With reference to the first of these points the facts of the case are the following:

In Amphibia the permanent opening of the Müllerian duct is formed as an independent opening after the atrophy of the head-kidney.

In Elasmobranchii the original opening of the segmental duct forms the permanent opening of the Müllerian duct and no head-kidney appears to be formed.

In Birds the anterior of the three openings of the head-

---

[1] Loc. cit.

kidney remains as the permanent opening of the Müllerian duct.

With reference to the difficulties involved in there being apparently three different modes in which the permanent opening of the Müllerian duct is formed, we would suggest the following considerations:

The history of the development of the excretory system teaches us that primitively the segmental duct must have served as efferent duct both for the generative products and kidney secretion (just as the Wolffian duct still does for the testicular products and secretion of the Wolffian body in Elasmobranchii and Amphibia); and further, that at first the generative products entered the segmental duct from the abdominal cavity by one or more of the abdominal openings of the kidney (almost certainly of the head-kidney). That the generative products did not enter the segmental duct at first by an opening specially developed for them appears to us to follow from Dohrn's principle of the transmutation of function (Functionswechsel). As a consequence (by a process of natural selection) of the segmental duct having both a generative and a urinary function, a further differentiation took place, by which that duct became split into two—a ventral Müllerian duct and dorsal Wolffian duct.

The Müllerian duct without doubt was continuous with the head-kidney, and so with the abdominal opening or openings of the head-kidney which served as generative pores. At first the segmental duct was probably split longitudinally into two equal portions, but the generative function of the Müllerian duct gradually impressed itself more and more upon the embryonic development, so that, in the course of time, the Müllerian duct developed less and less at the expense of the Wolffian duct. This process appears partly to have taken place in Elasmobranchii, and still more in Amphibia; the Amphibia offering in this respect a less primitive condition than Elasmobranchii; while in Aves it has been carried even further. The abdominal opening no doubt also became specialised. At first it is quite possible that more than one abdominal opening may have served for the generative products; one of which, no doubt, eventually came to function alone. In Amphibia the specialisation of the opening appears to have gone so far that it no longer has any relation to the head-kidney, and even develops after the atrophy of the head-kidney. In Elasmobranchii, on the other hand, the functional opening appears at a period when we should expect the head-kidney to develop. This state is very possibly the result of a differentiation (along a different line to that in Amphibia) by which the head-kidney gradually ceased to become developed, but by which the primitive opening (which in the development of the head-kidney used to be divided into several pores leading into the body cavity) remained undivided and served as the abdominal aperture of the Müllerian duct. Aves, finally, appear to have become differentiated along a third line; since in their ancestors the anterior pore of the head-kidney appears to have become specialised as the permanent opening of the Müllerian duct.

With reference to the posterior position of the head-kidney in Aves we have only to remark, that a change in position of the head-kidney might easily take place after it acquired an independent development. The fact that it is slightly behind the glomerulus would seem to indicate, on the one hand, that it has already ceased to be of any functional importance; and, on the other, that the shifting has been due to its having a connection with the Müllerian duct.

We have made a few observations on the development of the Müllerian duct in *Lacerta muralis,* which have unfortunately led us to no decided conclusions. In a fairly young stage in the development of the Müllerian duct (the youngest we have met with), no trace of a head-kidney could be observed, but the character of the abdominal opening of the Müllerian duct was very similar to that figured by Braun.[1] As to the backward growth of the Müllerian duct, we can only state that the solid point of the duct in the young stages is in contact with the wall of the Wolffian duct, and the relation between the two is rather like that figured by Fürbringer (Pl. I, figs. 14-15) in Amphibia.

---

[1] Loc. cit.

On the EARLY DEVELOPMENT *of the* LACERTILIA, *together with some* OBSERVATIONS *on the* NATURE *and* RELATIONS *of the* PRIMITIVE STREAK. By F. M. BALFOUR, M.A., F.R.S., Fellow of Trinity College, Cambridge. (With Plate III.)

TILL quite recently no observations were recorded on the early developmental changes of the reptilian ovum. Not long ago Professors Kupffer and Benecke published a preliminary note on the early development of *Lacerta agilis* and *Emys Europea*.[1] I have myself also been able to make some observations on the embryo of *Lacerta muralis*. The number of my embryos has been somewhat limited, and most of those which I have had have been preserved in bichromate of potash, which has turned out a far from satisfactory hardening reagent. In spite of these difficulties I have been led on some points to very different results from those of the German investigators, and to results which are more in accordance with what we know of other Sauropsidan types. I commence with a short account of the results of Kupffer and Benecke.

Segmentation takes place exactly as in birds, and the resulting blastoderm, which is thickened at its edge, spreads rapidly over the yolk. Shortly before the yolk is half enclosed a small embryonic shield (area pellucida) makes its appearance in the centre of the blastoderm, which has, in the meantime, become divided into two layers. The upper of these is the epiblast, and the lower the hypoblast. The embryonic shield is mainly distinguished from the remainder of the blastoderm by the more columnar character of its constituent epiblast cells. It is somewhat pyriform in shape, the narrower end corresponding with the future posterior end of the embryo. At the narrow end an invagination takes place, which gives rise to an open sac, the blind end of which is directed forwards. The opening of this sac is regarded by the authors as the blastopore. A linear thickening of epiblast arises in front of the blastopore, along the median line of which the medullary groove soon appears. In the caudal region the medullary folds spread out and enclose between them the blastopore, behind which they soon meet again. On the conversion of the medullary groove into a closed canal the blastopore becomes obliterated. The mesoblast grows out from the lip of the blastopore as four masses. Two of these are lateral: a third

---

[1] 'Die Erste Entwicklungsvorgänge am Ei der Reptilien,' Königsberg, 1878.

is anterior and median, and, although at first independent of the epiblast, soon attaches itself to it, and forms with it a kind of axis-cord. A fourth mass applied itself to the walls of the sac formed by invagination.

With reference to the very first developmental phenomena my observations are confined to two stages during the segmentation.[1] In the earliest of these the segmentation was about half completed, in the later one it was nearly over. My observations on these stages bear out generally the statements of Kupffer and Benecke. In the second of them the blastoderm was already imperfectly divided into two layers—a superficial epiblastic layer formed of a single row of cells, and a layer below this several rows deep. Below this layer fresh segments were obviously being added to the blastoderm from the subjacent yolk.

Between the second of these blastoderms and my next stage there is a considerable gap. The medullary plate is just established, and is marked by a shallow groove which becomes deeper in front. A section through the embryo is represented in Pl. III, Series A, fig. 1. In this figure there may be seen the thickened medullary plate with a shallow medullary groove, below which are two independent plates of mesoblast (*me. p.*), one on each side of the middle line, very imperfectly divided into somatopleuric and splanchnopleuric layers. Below the mesoblast is a continuous layer of hypoblast (*hy.*), which develops a rod-like thickening along the axial line (*ch.*). This rod becomes in the next stage the notochord. Although this embryo is not well preserved I feel very confident in asserting the continuity of the notochord with the hypoblast at this stage.

At the hind end of the embryo is placed a thickened ridge of tissue which continues the embryonic axis. In this ridge all the layers coalesce, *and I therefore take it to be equivalent to the primitive streak of the avian blastoderm.* It is somewhat triangular in shape, with the apex directed backward, the broad base placed in front.

At the junction between the primitive streak and the blastoderm is situated a passage, open at both extremities, leading from the upper surface of the blastoderm obliquely forwards to the lower.

The dorsal and anterior wall of this passage is formed of a distinct epithelial layer, continuous at its upper extremity with the epiblast, and at its lower with the notochordal plate, so that it forms a layer of cells connecting together the epiblast and hypoblast. The hinder and lower wall of the passage is formed by the cells of the primitive streak, which only assume a columnar form

---

[1] For these two specimens, which were hardened in picric acid, I am indebted to Dr. Kleneinberg.

near the dorsal opening of the passage (*vide* fig. 4). This passage is clearly the blind sac of Kupffer and Benecke, who, if I am not mistaken, have overlooked its lower opening. As I hope to show in the sequel, it is also the equivalent of the neurenteric passage, which connects the neural and alimentary canals in the Icthyopsida, and therefore represents the blastopore of Amphioxus Amphibians, &c.

Series A, figs. 2, 3, 4, 5, illustrate the features of the passage and its relation to the embryo.

Fig. 2 passes through the ventral opening of the passage. The notochordal plate (*ch'.*) is vaulted over the opening, and on the left side is continuous with the mesoblast as well as the hypoblast. Figs 3 and 4 are taken through the middle part of the passage (*ne.*), which is bounded above by a continuation of the notochordal plate, and below by the tissue of the primitive streak. The hypoblast (*hy.*), in the middle line, is imperfectly fused with the mesoblast of the primitive streak, which is now continuous across the middle line. The medullary groove has disappeared, but the medullary plate (*mp.*) is quite distinct.

In fig. 5 is seen the dorsal opening of the passage (*ne.*). If a section behind this had been figured, as is done for the next series (B), it would have passed through the primitive streak, and, as in the chick, all the layers would have been fused together. The epiblast in the primitive streak completely coalesces with the mesoblast; but the hypoblast, though attached to the other layers in the middle line, can always be traced as a distinct stratum.

Fig. B is a surface view of my next oldest embryo. The medullary groove has become much deeper, especially in front. Behind it widens out to form a space equivalent to the sinus rhomboidalis of the embryo bird. The amnion forms a small fold covering over the cephalic extremity of the embryo, which is deeply embedded in the yolk. Some somites (protovertebræ) were probably present, but this could not be made out in the opaque embryo.

The woodcut (fig. 1) represents a diagrammatic longitudinal

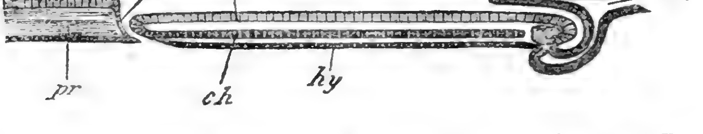


FIG. 1.—Diagrammatic longitudinal section of an embryo of Lacerta. *pp.* Body cavity. *am.* Amnion. *ne.* Neurenteric canal. *ch.* Notochord. *hy.* Hypoblast. *ep.* Epiblast. *pr.* Primitive streak.

section through this embryo, and the sections belonging to Series B illustrate the features of the hind end of the embryo and of the primitive streak.

As is shown in fig. 1, the notochord (*ch.*) has now throughout the region of the embryo become separated from the subjacent hypoblast, and the lateral plates of mesoblast are distinctly divided into somatic and splanchnic layers. The medullary groove is continued as a deepish groove up to the opening of the neurenteric passage, which thus forms a perforation in the floor of the hinder end of the medullary groove (*vide* Series B, figs. 2, 3, and 4).

The passage itself is somewhat shorter than in the previous stage, and the whole of it is shown in a single section (fig. 4). This section must either have been taken somewhat obliquely, or else the passage have been exceptionally short in this embryo, since in an older embryo it could not all be seen in one section.

The front wall of the passage is continuous with the notochord, which for two sections or so in front remains attached to the hypoblast (figs. 2 and 3). Behind the perforation in the floor of the medullary groove is placed the primitive streak (fig. 5), where all the layers become fused together, as in the earlier stage. Into this part a narrow diverticulum from the end of the medullary groove is continued for a very short distance (*vide* fig. 5, *mc.*).

The general features of the stage will best be understood by an examination of the diagrammatic longitudinal section, represented in woodcut, fig. 1. In front is shown the amnion (*am.*), growing over the head of the embryo. The notochord (*ch.*) is seen as an independent cord for the greater part of the length of the embryo, but falls into the hypoblast shortly in front of the neurenteric passage. The neurenteric passage is shown at *ne.*, and behind it is shown the primitive streak.

In a still older stage, represented in surface view on Pl. III, fig. C, medullary folds have nearly met above, but have not yet united. The features of the passage from the neural groove to the hypoblast are precisely the same in the embryo just described, although the lumen of the passage has become somewhat narrower. There is still a short primitive streak behind the embryo.

The neurenteric passage persists but a very short time after the complete closure of the medullary canal. It is in no way connected with the allantois, as conjectured by Kupffer and Benecke, but the allantoïs is formed, as I have satisfied myself by longitudinal sections of a later stage, in the manner already described by Dobrynin, Gasser, and Kölliker for the bird and mammal.

The general results of Kupffer's and Benecke's observations, with the modifications introduced by my own observations, are as follows:—After the segmentation and the formation of the embryonic shield (area pellucida) the blastoderm becomes distinctly divided into epiblast and hypoblast.[1] At the hind end of the shield a somewhat triangular primitive streak is formed by the fusion of the epiblast and hypoblast with a number of cells between them, which are probably derived from the lower rows of the segmentation cells. At the front end of the streak a passage arises, open at both extremities, leading obliquely forwards through the epiblast to the space below the hypoblast. The walls of the passage are formed of a layer of columnar cells continuous both with epiblast and hypoblast. In front of the primitive streak the body of the embryo becomes first differentiated by the formation of a medullary plate, and at the same time there grows out from the primitive streak a layer of mesoblast, which spreads out in all directions between the epiblast and hypoblast. In the axis of the embryo the mesoblast plate is stated by Kupffer and Benecke to be continuous across the middle line, but this appears very improbable. In a slightly later stage the medullary plate becomes marked by a shallow groove, and the mesoblast of the embryo is then undoubtedly constituted of two lateral plates, one on each side of the median line. In the median line the notochord arises as a ridge-like thickening of the hypoblast which becomes very soon quite separated from the hypoblast, except at the hind end, where it is continued into the front wall of the neurenteric passage. It is interesting to notice the remarkable relation of the notochord to the walls of the neurenteric passage. More or less similar relations are also well marked in the case of the goose and the fowl (Gasser),[2] and support the conclusion deducible from the lower forms of vertebrata, that the notochord is essentially hypoblastic.

The passage at the front end of the primitive streak forms the posterior boundary of the medullary plate, though the medullary groove is not at first continued back to it. The anterior wall of this passage connects together the medullary plate and the notochordal ridge of the hypoblast. In the succeeding stages the medullary groove becomes continued back to the opening of the passage, which then becomes enclosed in the medullary folds, and forms a true neurenteric passage. It becomes narrowed as the medullary folds finally unite to form the medullary canal, and eventually disappears.

I conclude this paper with a concise statement of what

---

[1] This appears to me to take place before the formation of the embryonic shield.

[2] Gasser, 'Der Primitivstreifen bei Vogelembryonen,' Marburg, 1878.

appears to me the probable nature of the much-disputed organ, the primitive streak, and of the arguments in support of my view.

In a paper on the primitive streak in the 'Quart. Journ. of Mic. Sci.,' in 1873 (p. 280), I made the following statement with reference to this subject:—"It is clear, therefore, that the primitive groove must be the rudiment of some ancestral feature. . . . . . . It is just possible that it is the last trace of that involution of the epiblast by which the hypoblast is formed in most of the lower animals."

At a later period, in July, 1876, after studying the development of Elasmobranch fishes, I enlarged the hypothesis in a review of the first part of Prof. Kölliker's 'Entwicklungsgeschichte.' The following is the passage in which I speak of it:[1]

"In treating of the exact relation of the primitive groove to the formation of the embryo, Professor Kölliker gives it as his view that though the head of the embryo is formed independently of the primitive groove, and only secondarily unites with this, yet that the remainder of the body is without doubt derived from the primitive groove. With this conclusion we cannot agree, and the very descriptions of Professor Kölliker appear to us to demonstrate the untenable nature of his results. We believe that the front end of the primitive groove at first occupies the position eventually filled by about the third pair of protovertebræ, but that as the protovertebræ are successively formed, and the body of the embryo grows in length, the primitive groove is carried further and further back, so as always to be situated immediately behind the embryo. As Professor Kölliker himself has shown it may still be seen in this position even later than the fortieth hour of incubation.

"Throughout the whole period of its existence it retains a character which at once distinguishes it in sections from the medullary groove.

"Beneath it the epiblast and mesoblast are *always fused*, though they are always separate elsewhere; this fact, which was originally shown by ourselves, has been very clearly brought out by Professor Kölliker's observations.

"The features of the primitive groove which throw special light on its meaning are the following:

"(1.) It does not enter directly into the formation of the embryo.

"(2.) The epiblast and mesoblast always become fused beneath it.

"(3.) It is situated immediately behind the embryo.

---

[1] 'Journal of Anat. and Phys.,' vol. x, pp. 790 and 791. Compare also my monograph on 'Elasmobranch Fishes,' note on p. 68.

"Professor Kölliker does not enter into any speculations as to the meaning of the primitive groove, but the above-mentioned facts appear to us clearly to prove that the primitive groove is a rudimentary structure, the origin of which can only be completely elucidated by a knowledge of the development of the Avian ancestors.

"In comparing the blastoderm of a bird with that of any anamniotic vertebrate, we are met at the threshold of our investigations by a remarkable difference between the two. Whereas in all the lower vertebrates the embryo is situated at the *edge* of the blastoderm, it is in birds and mammals situated in the centre. This difference of position at once suggests the view that the primitive groove may be in some way connected with the change of position in the blastoderm which the ancestors of birds must have undergone. If we carry our investigations amongst the lower vertebrates a little further, we find that the Elasmobranch embryo occupies at first the normal position at the edge of the blastoderm, but that in the course of development the blastoderm grows round the yolk far more slowly in the region of the embryo than elsewhere. Owing to this, the embryo becomes left in a bay, the two sides of which eventually meet and coalesce in a linear fashion immediately behind the embryo, thus removing the embryo from the edge of the blastoderm and forming behind it a linear streak not unlike the primitive streak. We would suggest the hypothesis that the primitive groove is a rudiment which gives the last indication of a change made by the Avian ancestors in their position in the blastoderm, like that made by Elasmobranch embryos when removed from the edge of the blastoderm and placed in a central situation similar to that of the embryo bird. On this hypothesis the situation of the primitive groove immediately behind the embryo, as well as the fact of its not becoming converted into any embryonic organ would be explained. The central groove might probably also be viewed as the groove naturally left between the coalescing edges of the blastoderm.

"Would the fusion of epiblast and mesoblast also receive its explanation on this hypothesis? We are of opinion that it would. At the edge of the blastoderm which represents the blastopore mouth of Amphioxus all the layers become fused together in the anamniotic vertebrates. So that if the primitive groove is in reality a rudiment of the coalesced edges of the blastoderm, we might naturally expect the layers to be fused there, and the difficulty presented by the present condition of the primitive groove would rather be that the hypoblast is not fused with the other layers than that the mesoblast is indissolubly united with the epiblast. The fact that the hypoblast is not fused with the other layers does not appear to us to be fatal to our hypothesis, and in Mammalia, where the primitive and medullary grooves present precisely the same relations as in birds, all three layers are, according to Hensen's account, fused together. This, however, is denied by Kölliker, who states that in Mammals, as in Birds, only the epiblast and mesoblast fuse together. Our hypothesis as to the origin of the primitive groove appears to explain in a fairly satisfactory manner all the peculiarities of this very enigmatical organ; it also relieves us from the necessity of accepting Professor Kölliker's explanation of the development of the mesoblast, though it does not, of course, render that explanation in any way untenable."

At a somewhat later period Rauber arrived at a more or less similar conclusion, which, however, he mixes up with a number of opinions from which I am compelled altogether to dissent.[1]

The general correctness of my view, as explained in my second quotation, appears to me completely established by Gasser's beautiful researches on the early development of the chick and goose,[2] and by my own observations just recorded on the lizard. While at the same time the parallel between the blastopore of Elasmobranchii and of the Sauropsida, is rendered more complete by the discovery of the neurenteric passage in the latter group, which was first of all made by Gasser.

The following paragraphs contain a detailed attempt to establish the above view by a careful comparison of the primitive streak and its adjuncts in the amniotic vertebrates with the blastopore in Elasmobranchii.

In Elasmobranchii the blastopore consists of the following parts:—(1), a section at the end of the medullary plate, which becomes converted into the neurenteric canal;[3] (2), a section forming what may be called the yolk blastopore, which eventually constitutes a linear streak connecting the embryo with the edge of the blastoderm (*vide* my monograph on Elasmobranch fishes, pp. 68 and 81). In order to establish my hypothesis on the nature of the primitive streak, it is necessary to find the representatives of both these parts in the primitive streak of the amniotic vertebrates. The first section ought to appear as a passage from the neural to the enteric side of the blastoderm at the posterior end of the medullary plate. At its front edge the epiblast and hypoblast should be continuous, as they are at the hind end of the embryo in Elasmobranchii, and,

---

[1] "Primitivrinne u. Urmuxd," 'Morphologisches Jahrbuch.,' Band ii, p. 551.

[2] Gasser, 'Der Primitivstreifen bei Vogelembryonen,' Marburg, 1878.

[3] I use this term for the canal connecting the neural and alimentary tract, which was first discovered by Kowalevsky.

finally, the passage should, on the closure of the medullary groove, become converted into the *neurenteric canal.* All these conditions are exactly fulfilled by the opening at the front end of the primitive streak of the lizard (*vide* woodcut, fig. 1). In the chick there is at first no such opening, but, as I hope to show in a future paper, it is replaced by the epiblast and hypoblast falling into one another at the front end of the primitive streak. At a later period, as has been shown by Gasser,[1] there is a distinct rudiment of the neurenteric canal in the chick, and a complete canal in the goose. Finally, in mammals, as has been shown by Schäfer[2] for the guinea-pig, there is at the front end of the primitive streak a complete continuity between epiblast and hypoblast. The continuity of the epiblast and hypoblast at the hind end of the embryo in the bird and the mammal is a rudiment of the continuity of these layers at the dorsal lip of the blastopore in Elasmobranchii, Amphibia, &c. The second section of the blastopore in Elasmobranchii or yolk blastopore is, I believe, partly represented by the primitive streak. The yolk blastopore in Elasmobranchii is the part of the blastopore belonging to the yolk sac as opposed to that belonging to the embryo, and it is clear that the primitive streak cannot correspond to the whole of this, since the primitive streak is far removed from the edge of the blastoderm long before the yolk is completely enclosed. Leaving this out of consideration the primitive streak, in order that the above comparison may hold good, should satisfy the following conditions:

1. It should connect the embryo with the edge of the blastoderm.
2. It should be constituted as if formed of the fused edges of the blastoderm.
3. The epiblast of it should eventually not form part of the medullary plate of the embryo, but be folded over on to the ventral side.

The first of these conditions is only partially fulfilled, but, considering the rudimentary condition of the whole structure, no great stress can, it seems to me, be laid on this fact.

The second condition seems to me very completely satisfied. Where the two edges of the blastoderm become united we should expect to find a complete fusion of the layers such as takes place in the primitive streak; and the fact that in the primitive streak the hypoblast does not so distinctly coalesce with the mesoblast as the mesoblast with the epiblast cannot be urged as a serious argument against me.

---

[1] Loc. cit.

[2] "A contribution to the history of the development in the Guinea-pig," 'Journal of Anat. and Phys.,' vol. xi, pp. 332—336.

The growth outwards of the mesoblast from the axis of the primitive streak is probably a remnant of the invagination of the hypoblast and mesoblast from the lip of the blastopore in Amphibia, &c.

The groove in the primitive streak may with great plausibility be regarded as the indication of a depression which would naturally be found along the line where the thickened edges of the blastoderm became united.

With reference to the third condition, I will make the following observations. The neurenteric canal, as it is placed at the extreme end of the embryo, must necessarily, with reference to the embryo, be the hindermost section of the blastopore, and therefore the part of the blastopore apparently behind this can only be so owing to the embryo not being folded off from the yolk sac; and as the yolk sac is in reality a specialised part of the ventral wall of the body, the yolk blastopore must also be situated on the ventral side of the embryo.

Kölliker and other distinguished embryologists have believed that the epiblast of the whole of the primitive streak became part of the neural plate. If this view were correct, which is accepted even by Rauber, the hypothesis I am attempting to establish would fall to the ground. I have, however, no doubt that these embryologists are mistaken. The very careful observations of Gasser show that the part of the primitive streak adjoining the embryo becomes converted into the tail-swelling, and that the posterior part is folded in on the ventral side of the embryo, and, losing its characteristic structure, forms part of the ventral wall of the body. On this point my own observations confirm those of Gasser. In the lizard the early appearance of the neurenteric canal at the front end of the primitive streak clearly shows that here also the primitive streak can take no share in forming the neural plate.

The above considerations appear to me sufficient to establish my hypothesis with reference to the nature of the primitive streak, which has the merit of explaining, not only the structural peculiarities of the primitive streak, but also the otherwise inexplicable position of the embryo of the amniotic vertebrates in the centre of the blastoderm.

On CERTAIN POINTS *in the* ANATOMY *of* PERIPATUS CAPENSIS. By F. M. BALFOUR, M.A., F.R.S.[1]

THE discovery by Mr. Moseley[2] of a tracheal system in Peripatus must be reckoned as one of the most interesting results obtained by the naturalists of the "Challenger." The discovery clearly proves that the genus Peripatus, which is widely distributed over the globe, is the persisting remnant of what was probably a large group of forms, from which the present tracheate Arthropoda are descended.

The affinities of Peripatus render any further light on its anatomy a matter of some interest; and through the kindness of Mr. Moseley I have had an opportunity of making investigations on some well-preserved examples of *Peripatus capensis,* a few of the results of which I propose to lay before the Society.

I shall confine my observations to three organs. (1) The segmental organs, (2) the nervous system, (3) the so-called fat bodies of Mr. Moseley.

In all the segments of the body, with the exception of the first two or three postoral ones, there are present glandular bodies, apparently equivalent to the segmental organs of Annelids.

These organs have not completely escaped the attention of previous observers. The anterior of them were noticed by Grube,[3] but their relations were not made out. By Saenger,[4] as I gather from Leuckart's 'Bericht' for the years 1868-9, these structures were also noticed, and they were interpreted as segmental organs. Their external openings were correctly identified. They are not mentioned by Moseley, and no notice of them is to be found in the text-books. The observations of Grube and Saenger seem, in fact, to have been completely forgotten.

The organs are placed at the bases of the feet in two lateral divisions of the body-cavity shut off from the main central median division of the body-cavity by longitudinal septa of transverse muscles.

Each fully developed organ consists of three parts:

(1) A dilated vesicle opening externally at the base of a foot.

---

[1] From the 'Proceedings of the Cambridge Philosophical Society.'

[2] "On the Structure and Development of *Peripatus Capensis,*" 'Phil. Trans.,' vol. clxiv, 1874.

[3] "Bau von *Perip. Edwardsii,*" 'Archiv f. Anat. u. Phys.,' 1853.

[4] "Moskauer Naturforscher Sammlung," 'Abth. Zool.,' 1869.

(2) A coiled glandular tube connected with this and subdivided again into several minor divisions.

(3) A short terminal portion opening at one extremity into the coiled tube (2) and at the other, as I believe, into the body-cavity. This section becomes very conspicuous in stained preparations by the intensity with which the nuclei of its walls absorb the colouring matter.

The segmental organs of Peripatus, though formed on a type of their own, more nearly resemble those of the Leech than of any other form with which I am acquainted. The annelidan affinities shown by their presence are of some interest. Around the segmental organs in the feet are peculiar cells richly supplied with tracheæ, which appear to me to be similar to the fat bodies in insects. There are two glandular bodies in the feet in addition to the segmental organs.

The more obvious features of the nervous system have been fully made out by previous observers, who have shown that it consists of large-paired supraœsophageal ganglia connected with two widely separated ventral cords—stated by them not to be ganglionated. Grube describes the two cords as falling into one another behind the anus—a feature the presence of which is erroneously denied by Saenger. The lateral cords are united by numerous (5 or 6 for each segment) transverse cords.

The nervous system would appear at first sight to be very lowly organised, but the new points I believe myself to have made out, as well as certain previously known features in it, appear to me to show that this is not the case.

The following is a summary of the fresh points I have observed in the nervous system:

(1) Immediately underneath the œsophagus the œsophageal commissures dilate and form a pair of ganglia equivalent to the annelidan and arthropodan subœsophageal ganglia. These ganglia are closely approximated and united by 5 or 6 commissures. They give off large nerves to the oral papillæ.

(2) The ventral nerve cords are covered on their ventral side by a thick ganglionic layer,[1] and at each pair of feet they dilate into a small but distinct *ganglionic swelling*. From each ganglionic swelling are given off a pair of large nerves[2] to the feet; and the ganglionic swellings of the two cords are connected together by *a pair of commissures containing ganglion cells*.[3] The other com-

---

[1] This was known to Grube, loc. cit.

[2] These nerves were noticed by Milne Edwards, but Grube failed to observe that they were much larger than the nerves given off between the feet.

[3] These commissures were perhaps observed by Saenger (loc. cit.).

missures connecting the two cords together do not contain ganglion cells.

The chief feature in which Peripatus was supposed to differ from normal Arthropoda and Annelida, viz. the absence of ganglia on the ventral cords, does not really exist. In other particulars, as in the amount of nerve cells in the ventral cords and the completeness of the commissural connections between the two cords, &c., the organisation of the nervous system of Peripatus ranks distinctly high. The nervous system lies within the circular and longitudinal muscles, and is thus not in proximity with the skin. In this respect also Peripatus shows no signs of a primitive condition of the nervous system.

A median nerve is given off from the posterior border of the supraœsophageal ganglion to the œsophagus, which probably forms a rudimentary sympathetic system. I believe also that I have found traces of a paired sympathetic system.

The organ doubtfully spoken of by Mr. Moseley as a fat body, and by Grube as a lateral canal, is in reality a glandular tube, lined by beautiful columnar cells containing secretion globules, which opens by means of a non-glandular duct into the mouth. It lies close above the ventral nerve cords in a lateral compartment of the body-cavity, and extends backwards for a varying distance.

This organ may perhaps be best compared with the simple salivary gland of Julus. It is not to be confused with the slime glands of Mr. Moseley, which have their opening in the oral papillæ. If I am correct in regarding it as homologous with the salivary glands so widely distributed amongst the Tracheata, its presence indicates a hitherto unnoticed arthropodan affinity in Peripatus.

On some POINTS *in the* EARLY DEVELOPMENT *of the* COMMON NEWT. By W. B. SCOTT, B.A., Fellow of the College of New Jersey, Princeton, and HENRY F. OSBORN, B.A., Princeton. With Plates IV and V.

THE present paper records a series of observations on the development of *Triton tæniatus* (and partially also *T. cristatus*), made by the writers in the Morphological Laboratory of the University of Cambridge.

It deals chiefly: (1) with the formation and character of the germinal layers; (2) the development of the notochord; (3) the extension of the body cavity into the head, and the formation of mesoblastic somites in that region; (4) the development of the thyroid body.

With a view of making the following account as clear as possible, we have chosen a series of embryos showing the most important steps in development, and have designated the stages which they represent by letters in imitation of the plan adopted by Mr. Balfour in his 'Monograph on the Development of the Elasmobranch Fishes.' And we have further endeavoured to make these stages correspond to those of *Bombinator igneus*, as figured by Dr. Götte[1] in his great work. As might be expected, Triton in many ways shows a close resemblance to the Batrachian,[2] and yet at the same time it presents a number of curious and striking differences from that type. In order to elucidate these we have followed Dr. Götte's arrangement as far as practicable.

The preparation of the Triton embryos was attended with considerable difficulty. It was found in all cases advisable to remove the albumen from the ovum before hardening. The vitellus is quite liquid, and the vitelline membrane is so excessively delicate that this operation must be conducted with the greatest care; and as the albumen is permeated by several membranes, it was found necessary to cut these with fine scissors before the embryo could be with safety

---

[1] A. Götte, 'Entwickelungsgeschicte der Unke.'

[2] The term "Batrachia," is used in this paper in the restricted sense as equivalent to the *Anurous Amphibia.*

extracted. Many hardening reagents were experimented with—osmic acid, bichromate of potash, Müller's fluid, &c., but the most satisfactory one proved to be Kleinenberg's picric acid, with which nearly all the embryos described in the following pages were prepared. In those cases where the entire egg was hardened without previously removing the albumen, the results were most unsatisfactory. Kleinenberg's hæmatoxylin was the staining fluid employed for the sections.

A.

This includes embryos intermediate in age between Götte's figs. 39 and 40, taf. iii. The blastospore is quite small, a narrow groove, the "Rückenrinne," running forward some distance from its anterior edge. The medullary folds do not as yet appear in surface views. The ovum is still almost perfectly spherical in shape.

B (Unke, Taf. iii, figs. 40 and 41).

At this stage the medullary folds become well developed and very plainly marked. As yet they are widely separated. The medullary plate is formed, but the groove which divides it into two parts does not reach far forwards of the middle; or, at any rate, if present anteriorly, is extremely faint. The ovum has elongated very slightly, but still appreciably.

C (Taf. iii, fig. 42).

The medullary folds now become still more pronounced, and begin to approach each other. The point of closest approximation is in the region which will eventually become the neck, and here is the first point of contact, just as it is in the Batrachia. The medullary plate is plainly divided throughout. The elongation of the embryo is not much more marked than it was in the previous stage.

D (see Pl. V, fig. 16).

Up to this stage no important external differences between Triton and Bombinator are apparent, but now a number of points of divergence begin to be noticeable. The medullary folds have closed throughout the region of the trunk, but still remain open in the head. Posteriorly they separate to form a *sinus rhomboidalis ;* this does not seem to be merely a part of the canal which has not yet closed, but a genuine dilatation. It is either absent or very transitory in Bombinator. As the folds enclose the blastopore, which remains open till a much later period, the sinus gives a communication from the exterior to the alimentary canal. When the sinus closes there is still the communication between the neural and alimentary canals, which has now been observed in so many types (Amphioxus, Accipenser, Elasmobranchii, Bombinator, &c.). The elongation of the embryo becomes very decided, and one surface of it becomes nearly flat; in Bombinator this is the dorsal surface; in the Newt it is the ventral, so that the latter is curved over the yolk. This difference is due merely to the larger amount of food-yolk in the egg of the Urodele, and cannot be considered of any great morphological significance. The bearings of the increased quantity of food-yolk will be discussed further on.

E.

This stage includes embryos, perhaps not quite so far advanced as the one figured in Götte's Taf. iii, fig. 50. The closure of the medullary folds is now complete throughout, and the vesicles of the brain are obscurely marked. The cranial flexure is already decided, and the whole embryo is somewhat curved upon itself, causing the ventral surface to assume a concave outline (except posteriorly, where the large mass of yolk produces a bulge). A trace of the opening of the sinus is still apparent.

F (Taf. iii, fig. 52).

The ventral curvature now becomes stronger, as does also the cranial flexure. The curvature is in an opposite direction to that taken by Bombinator. The vesicles of the brain are very distinct, and the optic vesicles which commenced in the last stage are now remarkably large, much more conspicuous than in the Bombinator of corresponding age. Another difference presents itself in the fact that in the latter the optic vesicle is an elongated oval, while in the former it is hemispherical. The rudiments of the fifth and seventh pairs of cranial nerves appear as buds from near the dorsal part of the hind brain, higher up than in Bombinator. A few protovertebræ have been formed. Up to this time there has been little or no increase in absolute size, the changes in form being produced by the elongation and narrowing of the embryo.

G.

In this stage the cranial flexure is carried further, and the head, as a whole, has taken a spherical shape, very different from the shape assumed by the Batrachian head. The rudiments of the visceral arches appear, and the tail begins to bud out from the yolk sac as an unsegmented mass of mesoblast. The number of somites has increased.

H (Taf. iii, fig. 53).

The elongation of the embryo has now progressed to a very considerable extent. The cerebral hemispheres bud out as an unpaired rudiment from the forebrain. Four visceral arches and three clefts have been formed. The tail has elongated somewhat, and is still unsegmented. We have been unable to discover anything of the suckers or horny teeth found in the Batrachian larvæ.

I (Taf. iii, fig. 54). (See also Pl. V, fig. 17).

This stage exhibits a general advance in development, but the only new feature is the appearance of the involution for the mouth. This is transversely elongated, differing from the mouth involution of Bombinator. The head shows swellings, which correspond in position to those which Götte has named, respectively, kidney swelling, lateral nerve, seventh and fifth nerves, auditory vesicle, and Gasserian ganglion; but, owing to the fact that the curvature is in the opposite direction, these organs are separated by wider intervals than in Bombinator.

We shall have occasion to refer to one or two later stages (K and L), which are marked by general increase in size, the formation of the lens, and the appearance of the external gills.

Segmentation and Formation of the Layers.

We have not succeeded in securing a complete series of specimens showing all the stages of segmentation, but from those which we have observed there can be little doubt that it proceeds very much in the same manner as in the Frog. Segmentation is asymmetrical, and this characteristic begins to appear at a very early period. The earliest stage we have seen shows two longitudinal furrows, which cut each other at right angles at the upper part of the egg, and passing down the sides, gradually fade and disappear before reaching the lower pole. The food-yolk even at this period preponderates in the lower part of the egg, and thus prevents the yolk-division taking place so rapidly as it does above. These furrows may be compared to two meridians on a globe; the next one (judging from the analogy of the Frog) represents the equatorial furrow in Amphioxus, but, for the reason above stated, it is much nearer to the upper pole than to the lower and this gives at once the distinction of larger and smaller blastomeres. The smaller blastomeres grow round the ovum over the larger, and bear the same relation to them as they do in the Frog. The segmentation cavity appears early, and from the very first its roof is only one cell thick, just as in the case of the Lamprey. As we shall see later the epiblast is at first composed of one layer, and hence the roof of the cavity is covered by epiblast only. In the Elasmobranch Fishes the roof of the cavity is formed by lower layer cells also, and this Mr. Balfour explains by the increase in the quantity of food-yolk in the cells, compelling them to creep up the sides of the cavity. Although there is proportionately more food material in the Newt's egg than in that of the Frog the increase is relatively small and does not affect the position of the cells. The only difference between the two at this stage consists in the fact that the roof of the cavity in the Frog is two or more cells thick, and in the Newt only one. In short, the ovum of the latter resembles the morula of Amphioxus with a large amount of food material stored away in its lower part. Judging from the descriptions of Calberla, it is in no way different from the ovum of Petromyzon of corresponding age. The floor of the segmentation cavity, as in all ova which contain food-yolk, is formed by the upper layer of yolk-cells from which, eventually, the ventral epithelium of the alimentary canal is in part derived.

The next step in development is, as in the Batrachians, a process of invagination, and, as in them, it is an unsymmetrical invagination. The disturbing cause is in both cases the presence of the food-yolk below. Owing to the fact that the food to be made available must be placed upon the ventral side of the body, the invagination must in this region take place very slowly or not at all. By this simple consideration Mr. Balfour explains the unsymmetrical gastrula of the higher Vertebrates.

At the period when our study of the two lower layers proper begins, segmentation is complete; the lips of the blastopore are rapidly nearing each other; the epiblast consists of a single layer of partly columnar, partly wedge-shaped, cells, and has already in great measure attained those characters which persist throughout several of the following stages.

At the lip of the invagination (see Plate IV, fig. 2) there is a decided swelling produced, in part by a lengthening, in part by a reduplication of the cells, a histological change analogous to that which has been pointed out in the so-called embryonic rim in the Elasmobranchs.[1] The cells have a radiated arrangement, losing as they are reflected inwards their columnar character and becoming more spindle-shaped. As they approach the inner side of the lip they are quadrate, then oblong, then columnar, their outer ends abutting against the inner ends of the long epiblast cells. As the sections pass into the lateral region of the embryo, this relation is lost, and confluent with the forming hypoblast cells are the parent mesoblast cells. The latter may fairly be considered to arise actually from the point of invagination and not as a secondary splitting off from the hypoblast on either side.

Two longitudinal sections of an embryo at this period have been figured in Plate IV, figs. 2 and 3. Fig. 2 represents a section passing through the median line, and those changes in the epiblast at the lip of the blastopore which have been just referred to, may be followed. The alimentary canal has not proceeded far forwards, but the cells of the upper yolk are plainly forming the future hypoblast cells. The segmentation cavity is being pressed downwards; the section is in the median line behind and out of the median line in front. The reverse is true of the succeeding section (fig. 3), which represents the growth of the mesoblast at the sides of the invagination and the actual forward progress of the alimentary canal in the middle line. It illustrates the position and advancing obliteration of the segmentation cavity. Comparing the two sections, a very fair idea can be formed of the advance of the embryo in the early part of the stage (A).

The process at the *sides* of the median line in Triton is then homologous to that which Götte[2] represents as occurring in the median line in Bombinator, a construction which aids him in carrying out his peculiar views of the development of the notochord from the mesoblast.

Calberla,[3] on the contrary, describes as the immediate result of invagination, in *Rana temporaria*, the primary entoderm. This does not split in the median line, while at the sides it splits soon after formation, to give rise to the lateral plates of mesoderm. A fuller notice of his views will be given later.

---

[1] *Vide* Balfour, 'Elasmobranch Fishes,' chap. ii, p. 43.

[2] *Vide* Alexander Goette, "Entwickelungsgeschichte der Unke," 'Atlas,' Tafel. ii.

[3] E. Calberla, "Zur Entwickelung des Medullarrohres und der Chorda-dorsalis der Teliostier und Petromyzonteu," p. 261, 'Morphologischen Jahrbuch,' 3, 1877.

Our sections do not wholly accord with the observations of either of the above, for if it is clear that the invagination gives rise in the median line to a single layer of cells, it is equally clear that at the sides it gives rise to a double layer, namely, of mesoblast as well as hypoblast.

The process in Triton agrees then more closely with that occurring in the Elasmobranch Fishes,[1] where the lower layer cells, confluent with the reflected epiblast on either side of the axial line, form a layer of spherical cells above and columnar cells below, and the former is ultimately separated off as the mesoblast proper, while in the axial line the lower layer cells give rise simply to a columnar layer.

Now, turning to the transverse section of a Triton embryo Stage A (see Plate IV, fig. 4) we find that it adds still further probability to this view, for the relations of the layers fully accord with the above interpretation of the invagination.

Now, as concerns the further growth of the mesoblast, it results from the foregoing conclusions concerning the hypoblast that the mesoblast is never present across the axial line in the early stages. In transverse sections of Stage A it appears as two lateral plates extending on either side to a point just above the side limits of the alimentary canal. The layer where it is nearest the alimentary canal consists of small round cells, one or two deep, which can be readily distinguished from the adjacent hypoblast. These are the cells which we have just referred to as having resulted from invagination, and we shall speak of them hereafter as the primary mesoblast cells.

In conclusion, all the observations we have made favour the above interpretation, while none in any way disprove it.

Thus, at once three important distinctions are established between the development of the layers at the point of invagination in Triton and Bombinator, if we accept in full Dr. Götte's investigations of the latter. First: in Triton there is a decided thickening of the single layered epiblast as it approaches the point of invagination. In Bombinator there is none. Second: the resulting hypoblast in the axial line is in direct contact with the epiblast. There is no intervening mesoblast as in Bombinator. Third: the mesoblast is found in Triton as two lateral plates, and is not continuous across the middle.

These observations, coupled with those of Calberla, we think leave little doubt that Götte has mistaken the upper hypoblast cells for mesoblast, and thus at the start fallen into an

---

[1] *Vide* F. M. Balfour, 'Elasmobranch Fishes,' p. 49.

error which involves some of his subsequent conclusions in doubt.

Having thus briefly considered the origin of the two inner layers, as related to the phenomena of invagination, we shall return to the history of the epiblast from the beginning, and resume our discussion of the mesoblast and hypoblast in the subsequent pages.

General Features of the Epiblast.

When the epiblast can first properly be said to be formed, it consists of a single layer of very large quadrate cells, with large clear nuclei. In the next stage, when the invagination first commences, the cells have somewhat lengthened out, but are still very broad (Plate IV, fig. 1). When the invagination has progressed considerably, and the segmentation cavity has been much narrowed, we find that the cells have assumed the condition which they retain for some time after this. They are long, narrow, and columnar; most of them can be traced through the layer from one surface to the other without any change of size, although here and there several may be seen which have a wedge-shape, and alternate arrangement with their neighbours. The nuclei, however, are arranged in two rows, like those of the Elasmobranch epiblast. In general appearance, up to this time, the epiblast is more like that of Petromyzon than of any embryo which we have seen,[1] but the arrangement of the cells is somewhat more regular. For a short time, indeed, the appearance of the two is almost identical, but in the Newt the cells speedily become narrower, and more columnar in character, and the nuclei assume the alternate arrangement which is only faintly indicated in the Lamprey. During Stage A, when the medullary groove has begun to make its appearance, the middle line of the dorsal epiblast, exhibits a decided thinning to form the groove (Plate IV, fig. 4). But this grove is not at this period, nor do we find it afterwards, nearly so deep or so wide as it is in the Elasmobranchs.[2]

The next change of importance takes place during Stage B (Plate IV, fig. 5), when the medullary folds are well formed. These folds are caused by the multiplication of cells of the epiblast, which here becomes much thickened. Although the folds are several cells thick they show no indication of being separated into different layers. With the excep-

---

[1] See a paper by Calberla, 'Morph. Jahrbuch,' 1877, 3, taf. xii, fig. 7.

[2] Balfour, loc. cit., plate iv, fig. 8 a.

tion of the medullary plate the remainder of the epiblast shows no especial change from the condition seen in the preceding stage. In the medullary plate, on each side of the middle line, is a low rounded ridge (Plate IV, fig. 5), which is formed by the increase in length of the epiblast cells, and perhaps partly also by the wedging in of the mesoblast along these two lines.

The condition of the spinal cord at this period recalls the the condition of the same organ in the Batrachia of this age. For in the latter the nervous and epidermic layers fuse together into one indiscriminate mass, and do not separate again till much later. This separation takes place for the first time in Triton, not far from the age in which it reappears in the Batrachia. During Stage C sudden and rapid changes make their appearance. The medullary folds are now very prominent, and are composed of numerous elongated spindle- and wedge-shaped cells, while in many places the medullary plate shows a commencement of the same process (Plate IV, fig. 6). But as yet in neither of these regions are any distinct layers to be seen. The lateral epiblast is just beginning to separate into two layers; the process commences immediately outside of the medullary folds, and spreads down the sides of the embryo, until it has been completed all around (fig. 6). Plate V, fig. 9, shows a drawing on a larger scale of the point where such changes are going on most actively. Even with the aid of this we have not thoroughly satisfied ourselves as to the exact manner in which these changes are accomplished. Three suppositions may be made with regard to it—(1) that the upper layer splits off from the lower by a process of cell division; (2) that the wedge-shaped cells draw in their edges, and lying in alternate arrangement come to make two rows, one above the other; (3) that both of these have their share in the process. On the whole we rather incline to the latter opinion. In favour of the alternate decrement of length is the fact that for some time preceding the separation the nuclei of the cells are arranged in two alternate rows, very much as in the Elasmobranchs, while such an appearance as shown at the point *a*, fig. 9, looks as if it could only be cell division.

Turning to Stage D (Plate IV, fig. 7), we find that in the trunk region the medullary canal is completely closed, and the division of the epiblast carried entirely around the embryo, giving us two well-marked layers. These are composed of quadrate, somewhat flattened cells, of nearly equal size in both layers. The cells composing the spinal cord are numerous, elongated, wedge- or spindle-shaped; but even yet there is no indication of distinct layers.

As in the Bird, the Mammal, and the Elasmobranch Fish, the epithelium lining the spinal canal does not become differentiated till a considerably later period.

As a whole the spinal cord is now a hollow cylinder with very thick walls and a very small lumen. It presents a transversely oval section, and is somewhat indented on its lower surface by the pressure arising from the notochord. The epiblast has met and coalesced along the middle line above the canal, though a slight groove still shows the line of union.

From this time forward the outer layer of the general epiblast becomes flatter and flatter, while the inner layer grows more columnar. But in those parts of the skin which cover the brain both layers are composed of very much flattened cells (Pl. V, fig. 13). The inner or mucous layer, when once formed, is the active layer, and from it alone such structures as the lens of the eye are derived.

The primitive condition of the epiblast in Triton is an extremely interesting one, presenting in a somewhat unexpected manner great differences from that of the Frog. As is well known, in the latter animal the epiblast is double-layered from an extremely early period, the roof of the segmentation cavity being formed by two layers of cells, and by the time of invagination there is an outer stratum of a single row of flattened cells and an inner stratum of several rows of rounded cells, the epidermic and nervous layers of Stricker. "Both strata have a share in forming the general epiblast, and though eventually they partially fuse together, there can be little doubt that the horny layer of the adult epiblast, when such can be distinguished, 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 they also at first fuse together, though the epidermic layer probably separates itself again as the central epithelium of the spinal canal." (Balfour, loc. cit., p. 99.)

All this is very different from what we see in Triton. At first the epiblast is of one layer, and so remains for a considerable time; the mucous layer, when formed, consists of a single stratum of more or less columnar cells, and the epithelium of the spinal cord appears for the first time at a much later period. In short, the condition of the epiblast, except in the last respect, is more like that of *Petromyzon* than that of the *Batrachia*. It is, as might be expected, intermediate between the two types in many ways. In the Lamprey the division into two layers does not occur until a comparatively late period, some time after the larva has been hatched, while in the Newt it occurs as early as Stage c. In the Frog it is found from the first. Another respect in which the Newt is intermediate is the histological character of the layers. The Elasmobranch Fishes in this respect present an intermediate condition between the Lamprey and the Newt. In them also the epiblast is primarily single; the first change consists in the part which will give rise to the central nervous system, becoming several cells thick, but presenting no distinction into two layers. Eventually, later than in the Newt, earlier than in the Lamprey, the epiblast divides into mucous and epidermic layers. Both layers seem to enter into the formation of the organs of sense, while in the Amphibians the sense organs are formed exclusively, or almost so from the mucous layer, and in the Lamprey they are derived from the epiblast before its division into the layers.

These facts put us in a somewhat favorable position for the solution of the question as to whether the single- or double-layered epiblast is the primitive condition. We are decidedly of the opinion that the conclusion drawn by Mr. Balfour on p. 100 of his book on the Elasmobranchs is the correct one, viz. that the single-layered epiblast is the more primitive condition. He was not aware at that time of the difference existing between the Frog and the Newt in this regard, and so attributed the double layer to the Amphibians generally. But, as we have seen, it is confined to the Batrachians, a much more restricted group, and is, perhaps, also found in Osseous Fishes. Besides these it is found in no other groups of the animal kingdom, and, as Mr. Balfour points out, it is more probable that a particular feature of development should be thrown back to an earlier period than for the distinction between the two layers to be absolutely lost, and then to reappear at a later stage. This *à priori* consideration receives a great deal of support from the facts of the development of the Newt. By its aid we are enabled to arrange a series of steps of advancing differentiation of the epiblast from Amphioxus through the Marsipobranchs, the Elasmobranchs, and the Newt, to the Batrachians.

The steps of this progression have been already stated, but it may be well to summarise them. (1.) Amphioxus has an epiblast consisting at first of short columnar cells in a single row. These afterwards begin to flatten out, and in the adult are very much flattened, *but never constitute more than a* *single row.* The medullary plate is the only epiblastic development which consists of more than one row of cells. This fact alone is of considerable weight in the question we are considering; and it should be borne in mind throughout the discussion that, in the most primitive vertebrate known, the epiblast is *permanently* single-layered. Into the peculiar method of the formation of the cerebro-spinal axis we need not enter.

(2.) In the Lamprey the epiblast does not divide until very late; in fact, not before the embryo has for some time been hatched (see Calberla, loc. cit., p. 264). This change takes place, however, in the region of the spinal cord before that organ has been formed, just as is the case in Amphioxus. The development of the nervous axis presents some peculiarities of a secondary nature. The sense organs are formed from the undivided epiblast.

(3.) The epiblast in the Elasmobranch Fishes separates into two layers much earlier than it does in the Lamprey, but still comparatively late in embryonic life, some time after the medullary canal has been completely closed, and several of the visceral clefts have appeared. According to Mr. Balfour it takes place at a stage slightly younger than K. The two layers are at first composed of flattened cells, but those of the inner stratum soon become columnar. "*Both layers apparently enter into the formation of the organs of sense.*"

(4.) In Triton the epiblast, though at first single, divides into its two parts at a very early stage, some time before the closing of the medullary canal (Stage c). When once formed the mucous layer becomes the active one and enters almost exclusively into the formation of the sense organs. So far as we are aware this is the only case as yet known in which there is a primitively single epiblast dividing early and delegating all its activity to one layer. It shows an approximation to the state of things found in the Frog.

(5.) In the Batrachia this is carried one step further and the two layers are distinguishable from the very first, even the roof of the segmentation cavity being double. The mucous or nervous layer, as in the Newt, enters alone into the formation of the organs of sense, &c. In short, almost the only difference in the matter of epiblast between the two classes of Amphibia lies in the *time* of its division.

Now, we are very far from asserting that these forms we have been considering represent the line of descent of the Batrachia; but we are decidedly of the opinion that they exhibit the steps of the process by which the epiblast of that group has reached its present complication. For this reason we are forced to the conclusion that even the early condition of the epiblast in the Batrachia is a secondary modification, and *that the primitive condition of the layer is single.*

As opposed to this conclusion may be adduced the fact that in the spinal cord of the Batrachia the two layers at first fuse together and at a later time reappear, as if the double-layered condition were a primary, the single-layered a secondary, and the reappearing double layer a tertiary stage in development. And further, that the first stage has been retained only in the Batrachia and (?) Osseous Fishes, and lost in other known vertebrates. But this appears unlikely, and standing entirely by itself, the above-mentioned fact cannot be considered to have any great value.

The Hypoblast.

We shall now continue the history of the hypoblast from Stage A onwards, until the development of the notochord. The embryo at this stage (see Pl. IV, fig. 4) is still spherical. In the section figured, which is in the anterior region of the embyro, the alimentary canal is broad and low, lined above by a deep single layer of columnar hypoblast cells. These are broader and longer than the epiblast cells above them, with nuclei of a spherical rather than oval shape. They are in contact with the epiblast broadly across the middle line, but at the sides, just below the two slight folds on either side of the medullary groove, the mesoblast begins to intervene as a single layer of small cells. Beneath these the hypoblast cells lose their columnar shape, and becoming more quadrate are gradually reflected around the sides of the alimentary canal, becoming continuous on the one hand with the quadrate yolk cells lining the alimentary canal below, on the other with the cells bounding the great mass of yolk. This continuity has been carefully represented in Pl. IV, fig. 4. Where the invagination cells cease would be difficult to state, owing to the fact that the bending down at the sides is a gradual process partly dependent upon the growth of the mesoblast.

The hypoblast can now be classed according to its development under two heads. (*a.*) The cells above the alimentary canal, which have arisen from invagination and are continuous with the reflected epiblast at the blastopore. This we shall call the invagination hypoblast. (*b.*) Those cells lining the alimentary canal below and those immediately bounding the yolk elsewhere, which arise by histological changes in the yolk cells proper. We shall refer to this as the yolk hypoblast.

The growth of the former class has been already considered in full. The latter arises by a slow process of metamorphosis in the peripheral yolk cells. The changes are not difficult to follow. The square yolk cells split as they approach the surface into long columnar or oblong cells, and at the same time a change takes place in the yolk spherules with which they are loaded, so that they show a greater avidity for the staining fluid. The large spherical nuclei of the yolk cells give place to the characteristic oval nuclei of the hypoblast. These primitive hypoblast cells assume more regular proportions as development proceeds. In the splitting off of the mesoblast which soon follows, fresh cells are constantly supplied from the yolk.

A further notice of Calberla's[1] views upon these points will perhaps not be out of place here. He considered the Lamprey embryo immediately after invagination to consist of two layers, the primary entoderm and the ectoderm. The former divides everywhere, except across the axial line, into the secondary entoderm and the mesoderm. Across the axial line the primary entoderm remains intact. He does not admit that the mesoderm arises even in part by invagination; but, still more important as it bears on the question under discussion, he does not include the outer yolk cells as part of the primary entoderm. So what we shall consider hereafter as the lateral mesoblast, he concluded, was joint mesoblast and hypoblast, not allowing that the outer yolk cells formed a distinct layer. The comparison has been inserted because at this period of its history the Lamprey presents many points in common with the Newt.

To resume the study of the hypoblast in Triton, it may be considered in the latter part of Stage C as forming a continuous layer around the yolk and completely enclosing the alimentary canal. By Stage B a very decided change has taken place (see Pl. IV, fig. 5). The section is in the head region where the alimentary tract has now reached a considerable size. The hypoblast is now only in contact with the epiblast in the median line, although the connection is such a close one that the three or four cells, still adhering, impinge so closely as to form a decided indentation in the epiblast—a feature which has been previously noticed in the Elasmobranch Fishes. The middle cells have also elongated and narrowed considerably, while those at the sides remain shorter; this results in a rounded upper outline. Laterally,

---

[1] *Vide* E. Calberla, loc. cit., on '*Petromyzon planeri*.'

they are still markedly continuous with the yolk hypoblast cells lining the alimentary canal and their lower margin arches upwards so as to form part of the lumen of the canal. This bending around of the hypoblast, which in Stage A was almost a straight line, into an arch of cells, must be partly attributed to a mechanical cause, viz. the rapid ingrowth of the mesoblast plates. Whatever the exact cause of this change it is well to note that no vital alteration has as yet taken place—the change is one merely of position. Elsewhere the hypoblast shows no new features.

Inasmuch as the interest in the hypoblast chiefly centres around the development of the notochord we shall consider the history of that organ by itself and complete the hypoblast later.

The Mesoblast.

It is evident from transverse sections in the latter part of Stage A (see Pl. IV, fig. 4) that the lateral plates of mesoblast have already attained a considerable thickness. At the junction of the invagination with the yolk hypoblast they are three or four cells deep, thinning out rapidly at the sides. In the anterior sections they barely extend below the middle, while behind they meet as a single layer of cells at the bottom, thus encircling the hypoblast except in the axial line above.

The lateral downward growth of the mesoblast in Triton is plainly not from the epiblast, for the epiblast has by this time formed a distinctly bounded single layer. There remain two modes in which it may *in great part* arise, (*a*) from the hypoblast; (*b*) independently of the hypoblast, from the yolk. This is of course excluding the mesoblast in the region of the alimentary canal which accompanies the process of invagination. If we consider, as we have reason to do from the analogy of the Frog, that the cells bounding the yolk form the primitive yolk hypoblast layer, we can only accept the former hypothesis. In the anterior section of Stage A the cells bounding the yolk below are as unquestionably hypoblastic as those bounding it above and at the sides. In other words, the hypoblast has formed as a distinct layer in contact with the epiblast below, before the mesoblast has appeared below at all. Moreover, at the sides, the down growth of the mesoblast is preceded plainly by a splitting off of the outer portion of the yolk hypoblast into large quadrate cells, and these in turn are seen in the process of subdivision. Although this growth seems to be at the expense of the hypoblast, it cannot be considered to arise altogether independently of the *down-*

growth of the invagination plates by a process of cell division, for the mesoblast does not arise at separate points, capping the hypoblast, but in direct continuity with the invagination mesoblast.

In the Elasmobranch Fishes, in which the origin of the mesoblast has been carefully observed, there is no doubt that this layer arises as two lateral masses, splitting off from the hypoblast at the same time that the latter arises as a distinct stratum from the lower layer cells. Here, however, the lateral plates do not form a continuous layer with the mesoblast which occasionally arises at the reflection of the epiblast at the sides, but are distinct from it.

Calberla,[1] as previously stated, explains the growth of the mesoderm (mesoblast) in the Lamprey, as an early splitting of the outer portion of the primary endoterm. This view fully confirms our interpretation of the lateral growth in Triton.

In Kowalevsky's earlier researches upon Amphioxus he fell into the error of supposing the mesoblast of double origin, hypoblastic and epiblastic, an error which he corrected later[2] by attributing this layer to a constriction off from the hypoblast, which occurs subsequent to the formation of the notochord. The simple invagination does not give rise to any but the two primitive layers. There can now be no doubt that the formation of the mesoblast is in all types a secondary phenomenon which is retarded in the simpler forms, and hastened in the more complex into an earlier period of development.

To review the features noticed in Stage A. The mesoblast arises by invagination as two lateral plates, and is never found across the median line. Subsequent growth is partly by cell division of these plates; mostly, however, at the expense of the hypoblast. The most rapid development is posteriorly, both in respect to thickness and downward growth. There is no tendency to split into somatic and splanchnic layers. By Stage B the mesoblast shows a very marked progress. It is now thickest immediately below the medullary plates, and causes that upward curve in the outline of the epiblast previously mentioned (Plate IV, fig. 5). At the same time the lateral plates have approached each other, bending the hypoblast downwards, so that now it is continuous with the epiblast only in the median line. The section figured is in the anterior part of the embryo near the head region. The cells appear larger than in the last stage,

---

[1] E. Calberla, loc. cit.

[2] *Vide* A. Kowalevsky, 'Archiv. fur Micros. Anatomie.' Band 13, p. 191.

near the axial line they are crowded together irregularly, but at either side the splitting into two single-celled layers begins to be evident. This splitting begins anteriorly and proceeds slowly backwards. In the posterior sections of the same embryo it is barely evident, although the cells show a tendency to arrange themselves in two rows. Plate IV, fig. 6, represents a section from the trunk region during Stage C, and shows that the splitting of the mesoblast extends slowly backwards. In this region the layer is now thinner than it is forwards, although the reverse of this is true of Stage A, where the mesoblast is thickest posteriorly. The proximal cells now begin to arrange themselves radially around the vertebral portion of the future body cavity, closely impinging against the epiblast, and tending to grow in above the primitive notochord. The body cavity does not extend beyond the medullary folds in this embryo, for here the two rows of cells suddenly terminate in a single row bending around the sides. In other respects the mesoblast shows no new features until Stage D. Sections of an embryo, during the latter part of Stage D, show that the neural canal has completely closed. The section figured in Plate IV, fig. 7, is in the anterior trunk region, here the mesoblast appears as two great triangular muscle plates, expanding above so as to fill the space formed by the fusion of the medullary canal, and enclosing the large body cavity. The two layers now extend completely around the embryo, but have not separated except in the upper region. In Stage F the division into somites has begun.

To conclude, there is one feature in the development of the mesoblast, which argues strongly for the fact that, mesoblastic invagination being begun, lateral growth sets in at once; that is, the cells formed by invagination are immediately supplemented by those growing down at the sides, of hypoblastic (yolk cell) origin. As evidence of this we find the mesoblast of the posterior sections meeting in the median line below, before it even reaches the ventral region anteriorly. In this single respect, the mesoblast develops more rapidly behind than in front. Subsequent to the formation of the alimentary canal, the greater energy of the embryo is directed to the head region, and all following growth is from before backwards. This is true of the thickening of the lateral plates, of the splitting into two layers, of the formation of the body cavity, and of the subsequent division into somites.

The Notochord.

In our description of the hypoblast, we considered the layer as classed under two heads, the invagination hypoblast, and the yolk hypoblast; it is with the former that the development of the notochord is concerned. The cells lying during Stage B between the mesoblast plates may be considered the primitive notochordal cells.

The first indication of the growth of the notochord in Triton (see Plate IV, fig. 5), is the tendency of the cells to take a radiated arrangement. We may now at the outset, point out three prominent features. First, the hypoblast consists of a single layer of columnar cells running from the epiblast above to the alimentary canal below. Second, these cells may be identified with the broad band of invagination cells which in Stage A were all in contact with the epiblast. They have been bent down by the ingrowth of the mesoblast above. Third, these cells are directly continuous at the sides with the yolk hypoblast.

In the Lamprey,[1] *Petromyzon planeri*, the relations of the hypoblast at this point to the epiblast and mesoblast are practically the same. There is the same close and broad contact with the epiblast, and the cells are of the same relative size. Here, as in Triton, the primary or invagination cells are alone concerned in the origin of the notochord.

In the Frog (*Rana temporaria*)[2] the primitive condition of the notochord is a great cubical mass of small cells, confluent with the epiblast above, and with the mesoblast at the sides. These do not all enter into the formation of the notochord, however, for at the time this organ begins to be constricted off, the lower cells form a hypoblastic lining to the alimentary canal. Götte's account of the first appearance of the notochord in the Frog (*Bombinator igneus*) differs widely, owing to the fact that he has mistaken the upper hypoblast cells for the mesoblast.

In the Elasmobranch Fishes[3] the arrangement is analogous, for the whole layer with the exception of a thin line of cells over the alimentary canal, enters into the notochord. The cells are at no time so widely in contact with the epiblast as in Triton; so the change preceding the formation of the notochord consists, first, in the lengthening, and then splitting of the cells into two lines placed end to end. The lower line thus formed is, however, mostly absorbed in the

---

[1] *Vide* E. Calberla, loc. cit.

[2] *Vide* E. Calberla, loc. cit., p. 260.

[3] *Vide* Balfour, loc. cit., p. 93.

formation of the organ, and is not, as in *Rana temporaria*, wholly expended in forming the upper layer of the alimentary canal. To return to Triton, it is well to notice here that the upper boundary of the alimentary canal is formed by the cells which will give rise to the notochord, and that the latter at this period actually contains part of the lumen of the canal.

Following the notochord into the succeeding stage, we find no marked changes (Pl. IV, fig. 6). The section taken from the middle region of the embryo presents much the same appearance. From this we infer that in common with the other organs, the notochord develops more rapidly forwards, and that the backward development is a slow one, for in Stage C the notochord is but little more advanced in the middle region of the embryo than it is in the anterior region in the preceding stage. The primitive features pointed out above remain constant.

Unfortunately there is a gap in our sections here, at least we have none by which we can trace the histological changes from the simple fold of hypoblast cells in Stage C, to the firm rod of radiating cells in the latter part of Stage D. There is no evidence of their splitting into two cells deep previous to this result as in the Lamprey and the Elasmobranchs. The exact process beyond the ascertaining of this point is of little real importance.

In Stage D (Pl. IV, fig. 7) the relations of this organ are not much altered, it still impinges against the epiblast above, and partly bounds the alimentary canal below, but the continuity with the hypoblast has been broken off, and the line of demarcation is plainly marked by the different character of the cells. The notochordal cells are subquadrate in shape, about twelve in number in a transverse section, and are arranged around a centre of their own. In other words, the notochord is now an independent body; at its sides below are the long narrow hypoblast cells which partially enclose it, and above are the mesoblast plates fully formed, which, however, show no tendency to surround it.

The notochord is now larger than at any subsequent stage. In its formed or permanent condition, it persists as a close granular mass in which we can sometimes detect cell division, sometimes not. (See Pl. V, fig. 8; figs. 12 and 13.) In Stage E an ingrowth of hypoblast below, cuts off its connection with the alimentary canal. In a much later period, Stage M, it has a vacuolated appearance; a branching network of connective tissue supporting prominent nuclei, an appearance which has been noticed in many other forms (Pl. IV, fig. 15).

This completes the interesting history of the development of the notochord. To summarise: The invagination hypoblast cells are first continuous as a single layer, wholly across the median line; those farthest from the three central cells are gradually pushed down by the ingrowth of the mesoblast. There is no tendency to split below. They are further reflected around until the lateral cells meet, and the continuity with the hypoblast is broken. It still impinges against the epiblast above, and forms the upper boundary of the alimentary canal below.

A comparison has already been instituted between the development of the notochord in Triton and its development in the Frog, the Lamprey, and the Elasmobranch Fishes. In important details the processes are very similar. To carry the comparison a step further, in Amphioxus the notochord is differentiated from the hypoblast before the mesoblast has become constricted off, and at the time that the medullary plate is closing in above.

Hensen has demonstrated, beyond doubt, that the notochord is of hypoblastic origin in the Guinea-pig; and that it probably arises in the same way in the Rabbit. Quite recently,[2] Mr. Balfour has shown that it has a similar derivation in the Lizard, *Lacerta muralis*.

In several respects the notochord arises in a simpler manner in Triton than in any of those forms in which the process has been clearly followed out. In that: first, the cells do not reduplicate vertically, as in the Elasmobranchs and the Lamprey, previous to the formation of the organ; second, when the organ is completely formed, it still bounds the alimentary canal below, as in neither of the other forms nor in the Frog; third, no portion splits off subsequently to form the hypoblast layer bounding the canal above, this layer appears from the sides.

It is difficult to judge from Kowalevsky's description, whether the whole depth of the layer bounding the canal above is absorbed by the notochord, or whether the lower portion remains as an upper lining of the canal, and the upper portion alone enters into the notochord. If the latter is the case, the Newt presents the simplest notochordal development known.

The evidence from all these forms points so strongly in one direction, as to amount almost to proof, that the study

---

[1] *Vide* Kowalevsky, loc. cit.

[2] *Vide* F. M. Balfour, this Journal, Vol. XIX, p. 3, New Series.

of the more important types which have not as yet been observed, and the clearing up of the doubts which still envelop other types, will fix the derivation of the notochord from the hypoblast as a law, rather than as a feature positive in some cases, and with an exceptional origin from the mesoblast in others.

The Hypoblast.

In Stage C the notochordal cells are continuous at the sides, with the layer of hypoblast lining the yolk (see Pl. IV, fig. 6). In Stage D this continuity is completely broken, the layer appears as a long narrow row of cells, flattened against the sides of the notochord, but not enclosing it below. Elsewhere this layer shows no new features. In Stage E, however (see Pl. V, fig. 8), the cells have grown down and meet below, completely surrounding the alimentary canal and shutting it off from the notochord. This process is interesting, as it shows that, while the original upper lining is mainly absorbed by the notochord, the permanent upper lining is formed from the yolk hypoblast cells, and that now almost the entire layer is formed of this secondary hypoblast, the bulk of the primary or invagination hypoblast having gone to the notochord. The hypoblast grows under the notochord, in much the same way in the Lamprey, but at a somewhat earlier stage. In most of the other forms there remains throughout, a thin layer of cells intervening between the notochord and the yolk.

Body Cavity and Somites of the Head.

As already mentioned, the growth of the mesoblast is from behind forward, and in Stage A (Pl. IV, fig. 4) we see that in the head region the mesoblastic plates do not meet ventrally. They gradually thin out forwards and end near the blind termination of the alimentary canal. At this period the mesoblast is quite thick, and is composed of numerous cells of spherical shape, but exhibits no tendency to become divided into somatic and splanchnic layers. In Stage B, however, the cells have arranged themselves into two layers, and quite a cavity has appeared between them (Pl. IV, fig. 5). As yet this change is confined to the head, and so there is a cavity in the head on each side of the middle line, contained between the somatic and splanchnic layers of the mesoblast. These cavities, therefore, are parts of the pleuro-peritoneal cavity, and when that is formed in the body, will be directly continuous with them. As in the

Elasmobranch Fishes,[1] the cavity in the head is formed at a period considerably before that at which it appears in the body. These two *head cavities* have no communication with each other, as the mesoblast in the head is in two separate masses. A longitudinal horizontal section (Pl. V, fig. 10) through an embryo slightly older than F shows this cavity *(pp.)* as an undivided slit bounded by columnar mesoblast cells. But when the first visceral cleft appears as an outgrowth from the hypoblast of the throat to join the external skin, this cavity is necessarily separated into two portions, one behind and one in front of the cleft. This cleft in the latest stages we have been able to observe never pierces the skin, but it lies close to it and so divides the mesoblast. The second cleft divides the cavity into three sections, and each succeeding one adds a fresh segment to the number. Of course this number is not so great as it is in the Elasmobranch Fishes.

The section in front of the first cleft presents some features which demand attention. It grows forward and becomes divided spontaneously into two portions, one of which lies close to the optic vesicle (Pl. V, fig. 11), and entirely in front of the mouth, while the second (2 *pp.*) is enclosed altogether in the mandibular arch. The first aortic arch (1*aa*) runs between these two sections and somewhat dorsal to them. We have not been able to make any satisfactory observations upon their relation to the branches of the fifth nerve, but from their position it seems in every way probable that they have much the same relations as those described by Mr. Balfour in the Elasmobranch Fishes. The first division shows a small lumen surrounded by a layer of short columnar cells; in longitudinal vertical sections (Pl. V, fig. 11, 1 *pp.*), it has a somewhat oval shape; in transverse sections (fig. 13, *pp.*) it has a transversally elongated shape, and the cavity in these sections is seen to be largest toward the middle line. During no period as late as Stage L could we find any trace of a ventral union between the anterior segments of each side, such as occurs in the Elasmobranchs. It may, however, occur later, as during Stage L they approach very closely. The second segment (Pl. XXI, fig. 11, 2 *pp.*) is considerably smaller than the first, and has a very small lumen. Its cavity also is lined with columnar cells, and forms a narrow slit running parallel to the first visceral cleft. The mandibular aortic arch lies just anterior to it instead of close to its inner side as in the Elasmobranchs.

The other segments of the head cavity lie in the visceral

---

[1] Balfour, loc. cit., p. 86.

arches, and show narrow cavities lined by columnar epithelium (Pl. XXI, fig. 12, 3 *pp*). They present no features of especial importance. We have not followed out the subsequent development of these segments, but in all probability their cells become transformed into muscle cells.

In the foregoing description there will be observed a very close similarity to what has been described for the Elasmobranchs; in fact, with some minor exceptions, and the one important one of the non-communication of the first pair of segments, Mr. Balfour's descriptions will apply equally well to our specimens. This is of the more interest, for Triton in this respect is very much more like the Elasmobranchs than it is like the Batrachians; a fact which is somewhat remarkable. In the Batrachians so carefully investigated by Dr. Götte,[1] there appears to be no head cavity formed at any period. On the other hand, two series of segments, an inner and an outer series, become formed, and are believed by Dr. Götte to correspond respectively to the vertebral and lateral plates of mesoblast which are developed in the trunk. The internal segments resemble the protovertebræ in shape, but are smaller; their walls develop into muscular fibres and represent the anterior continuation of the dorsal muscles. The external segments are contained in the visceral arches. In the anterior division of the head (Götte's Vorderkopf) there is only one pair of segments, as the division of the segment in front of the first visceral cleft does not seem to occur; the part contained in the mandibular arch is derived from the growth of the postero-lateral segments. The most anterior segment of all gives rise, as in the Elasmobranchs, to the muscles of the eye.

It is remarkable how very different all this is from the process observable in Triton. There are found in the posterior part of the head four segments which give rise to muscular fibres, as in Bombinator, and continue the dorsal muscle forwards. These may be equivalent to the four internal segments of the head of Bombinator, but they have no ventral continuations. They are more to be compared with segments in the posterior part of the head of the Elasmobranchs. With regard to the latter, Mr. Balfour says (p. 209), "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 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

---

[1] Unke, pp. 203-208, 216-229.

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 be a part of the trunk system of muscles which has to a certain extent overlapped the back of the head, but am inclined to accept the latter view." The appearances here described are very much like those to be seen in Triton, and we are not in a position to pronounce any more decided judgment upon them, than upon those of the Elasmobranchs; but taking into consideration Götte's figures we are rather inclined to consider them the axial segments of which the plate containing the head cavity is the lateral part. The chief differences between the two types of Amphibians lie in the cavities themselves, and the number of segments in the anterior part of the head.

Our researches do not, we regret to say, throw much new light upon that difficult morphological problem, the segmentation of the head. It is interesting to find that as in the Elasmobranchs there is one præ-oral segment, as might be expected to be the case if the head cavities afford any trustworthy guide to the number of head segments. Of course the number of postoral cavities is less than in the Elasmobranchs owing to the fewer gill clefts, but this is a feature which does not affect the question at issue.

Of whatever value these facts in the development of the Newt are considered, we think that they favour the views expressed by Mr. Balfour in p. 216 of his book. For these head cavities, if of morphological importance, might be anticipated to be fairly constant in character.

The Thyroid Body.

Pl. V, fig. 12, represents the earliest condition of the thyroid body which has fallen under our observation. In it we see that in the region of the mandibular arch there is a *solid* outgrowth of cells from the ventral wall of the alimentary cavity which has reached the inner layer of the epiblast. The latter has at the point of contact risen up slightly from the external layer leaving a small triangular space between them. In the next stage (fig. 13), the inner layer of epiblast has coalesced with the hypoblastic outgrowth and is discontinuous across the middle line. It is now difficult to determine where one layer begins and the other ends, so complete is their fusion. The external layer is never interrupted. Fig. 14 presents a rounded thickening of the fused mass, which is the next step in development.

The latest stage we have (somewhat later than M) shows the gland separated from the epiblast (Pl. V, fig. 15) which is now continuous across the middle line, but still connected with the ventral wall of the œsophagus by a cord of cells. The thyroid is now a solid cylindrical rod of considerable length, ending posteriorly near the ventral aorta; the section shows an aortic arch (1 *aa*) cut through longitudinally. The gland consists of an outer or cortical layer of columnar cells arranged radially, and an inner small kernel of rounded cells. As yet there is no trace of a lumen, or any division into lobules. Further than this we have not been able to follow its development, but have no reason to suppose that it presents any great peculiarities.

On the whole the thyroid body of the Newt corresponds quite closely in position and mode of development to the same body in the Elasmobranch Fishes; but there are some points of difference to which we should like to call particular attention. (1.) In the latter the diverticulum of the hypoblast is hollow in front and solid behind at first, and only subsequently becomes solid throughout, while in Triton we have not been able to discover any stage which shows a hollow outgrowth. The solidity, however, does not occur from any confused mass of cells, but from the fact that the two sides of the diverticulum are pressed closely together (Pl. V, figs. 12 and 13). Of course it is very possible that we have missed a stage in which the outgrowth was hollow; but if that is the case that condition must be a very transitory one. The difference is only one of detail in any case. (2.) Of much more importance is the fact that in the Elasmobranchs there is never found any indication of continuity between the hypoblast and epiblast, which at this period is still single layered. But the diverticulum is pressed very closely against the epiblast, presenting just the appearance of the first visceral cleft which does not perforate the skin.[1] (We do not wish to intimate by this comparison an opinion that the thyroid is a modified visceral cleft, because all diverticula from the throat to the external skin must look more or less alike.)

The account given by Dr. Götte[2] of the development of the thyroid in Bombinator is still more like our account than is that given by Mr. Balfour of the Elasmobranchs.

---

[1] Balfour, loc. cit., Plate XIV, fig. 5*a*, p. 223-5.

[2] Loc. cit., p. 667.

In Bombinator the thyroid "is formed from a pit of the hypoblast, which persists as the remains of an early depression of the hypoblast behind the mandibular arch, *produced by a fusion of the epiblast and hypoblast*" (Taf. vii, fig. 127-130, and Taf. xiii, xv, xvi, figs. 292 and 293.) At first it is connected anteriorly with the median division line which bisects that arch; after the disappearance of this the rudiment of the thyroid appears as a funnel-shaped diverticulum of the hypoblast and is free below. The fusion between the two layers, which in Triton persists for a considerable period and is seen throughout the length of the gland, here is confined to the anterior end, and remains only a short time.

W. Müller, in his account of the development of the thyroid body[1] in *Rana temporaria*, does not give any figures or descriptions leading us to suppose that he has observed this continuity of the layers.

We must confess that we ourselves are very much puzzled by the fusion of the epiblast and hypoblast at this point, and are unable to give any morphological explanation of its meaning. Is it not just possible that it may represent some shifting in the position of the mouth? but if so, we shall be obliged to abandon, for this form at least, the homology of the thyroid body with the endostyle of the Ascidians. We mention it with the hope of directing the attention of some morphologist, who will clear the matter up, to this curious and unexplained feature.

It may be of use to give a brief summary of the points which we have endeavoured to establish in this paper, before passing on to consider to what general conclusions these points lead us, if established.

1. As to *external features*, we have failed to find in Triton the suckers and horny teeth with which the Batrachian larva is furnished.

2. *Segmentation* proceeds in a manner much like that of the Frog, but the roof of the segmentation cavity is from the very first only one cell thick.

3. *An unsymmetrical invagination*, like that of the Frog and Lamprey, takes place, giving rise to one layer in the middle line, the hypoblast, and two at the sides, hypoblast and mesoblast. The invagination *mesoblast* is supplemented by other cells, which split off from the yolk hypoblast. These two lateral and disconnected masses of mesoblast are, we consider, the homologues of the paired hypoblastic diverticula in Amphioxus.

---

[1] Jenaische, 'Zeitschrift,' 1871, pp. 435-439.

4. The *epiblast* is at first composed of a single layer of columnar cells, which early separate into two rows, and of the two layers thus formed the inner becomes the active one, entering exclusively into the formation of the sense organs. In the spinal cord and brain the division into two layers does not take place till very much later.

5. The *hypoblast* is of two kinds, the invaginated and that which arises from the metamorphosed yolk-cells.

6. The *notochord* is of hypoblastic origin, and takes up the entire dorsal wall of the alimentary tract (except in the head) in its formation, fresh hypoblast growing from the sides below it. It becomes well formed and cylindrical in shape before any cell division takes place in it.

7. The *body-cavity* extends into the head, appearing in this region first. The head mesoblast becomes split into somites, which have the same relations and number (except so far as modified by the reduction of the visceral clefts) as in the Elasmobranchs, but do not seem to communicate below.

8. The *thyroid* body is formed by an outgrowth from the alimentary canal, the walls of which become continuous with the mucous layer of the epiblast; the continuity of the horny layer is not interrupted.

Conclusion.

If the statements in this paper prove to be well founded, they will give us some data for judging of the relationships of the two groups of Amphibia to each other, and to some lower types. The marked divergences from the Batrachian type which the Newt shows us point to the conclusion that the Urodeles and Batrachians have been separated for a very long period. And it is interesting to observe that, in those cases where the divergence is other than a mere matter of detail, it leads towards the Lamprey, and through that to Amphioxus. The opinion seems to be gaining ground that some such form as the Lamprey is the point toward which the Amphibia, the Elasmobranch, Ganoid, and Dipnoic fishes converge, and the more these types are investigated the better established appears this view. As yet, however, we are not in a position to pronounce upon it with even an approximation to certainty. The observations brought forward in this paper tend strongly, we think, in this direction, and we hope that future investigations upon the

Amphibia, the Ganoids, and especially the Dipnoi, will soon put the matter to a crucial test.

In conclusion, we must express our very sincere thanks to Mr. F. M. Balfour for his never-failing kindness and assistance to us while engaged in this work.

DEVELOPMENT *of the* KIDNEY *in its relation to the* WOLFFIAN BODY *in the* CHICK. By ADAM SEDGWICK, B.A., Scholar of Trinity College, Cambridge; Demonstrator in the Morphological Laboratory. (With Plates VI and VII.)

THIS paper contains an account of observations on the development of the excretory system of the chick, made with a view of elucidating the relation which the kidney bears to the Wolffian body.

The Wolffian body in the embryo chick attains to a very great development, but almost completely atrophies in the adult, a small part only persisting in the male as part of the testicular apparatus.

In the embryos of lower Vertebrates, viz. most of the Icthyopsida, there is present, similarly, an organ called the Wolffian body, which, however, much more completely persists in the adult, functioning in part as kidney and in part as semen carrier.

The separation into an urinary part and into a sexual part is much more complete in some forms than in others. In the Elasmobranchii, for instance, the posterior part of the embryonic Wolffian body gives rise in the adult to a well-developed gland, the kidney, while the anterior part attains a far less development; in fact, more or less retrogrades in the adult; but in the male a part of it enters into connection with the testis.

In the Amniota the case is different. In them an embryonic organ, called the Wolffian body, does not function at all in the adult as an excretory organ; it almost completely atrophies from its embryonic perfection, only a small part persisting in the adult male as the epidydimis. The organ which functions as kidney in the adult arises at a relatively late stage, and is not apparently, as in Elasmobranchs, a modified part of the hind end of the embryonic Wolffian body. What, then, is the kidney of the Amniota? Is it an organ which has arisen *de novo* in the Amniota, or can it, by a more accurate study of its development, be traced into relation with the embryonic excretory system? In other words, can any evidence be obtained by the study of development proving that the kidney of the chick phylogenetically has been modified from part of the same primitive organ as that from which the Wolffian body developed, as is the case in the Icthyopsida ?

To obtain an answer to these questions I have been obliged to make a close study of the earliest stages in the development of the kidney and Wolffian body. The results obtained with regard to the latter are so different from those obtained by the latest observers, that I have recorded them in full in the following account.

Peculiarities in the early development of the Avian Woffian body necessitated an examination of the early development of the Wolffian tubules in other Vertebrates. This examination I was enabled to make in the case of Elasmobranchii owing to the great kindness of Mr. Balfour, who placed at my disposal the whole of his Elasmobranch sections. The result of this examination was to convince me that the account given of the earliest stages in the development of the Elasmobranch Wolffian body is in some respects erroneous.

Before proceeding to an account of the observations made upon these heads it will be well to give a short historical account of the progress of our knowledge on this subject, *i.e.* the development of the Wolffian body and kidney.

The later views as to the homologies of the parts of the excretory system found in the different members of the Vertebrate group dates from the work of Balfour[1] and Semper[2] on the embryology of Elasmobranchs.

The independent discoveries of these two investigators gave an impulse to the study of the development of the organs in question in other animals, and as a result it has gradually become clearer as the embryology of more animals became known that a great similarity in the development of these organs characterised the Vertebrata.

The earlier observers, Remak[3] and Rathke,[4] maintained that the tubules of the Wolffian body developed independently of the Wolffian duct in a blastema of mesoblast cells adjoining the inner side of the duct.

Waldeyer, in his well-known work,[5] asserted from his observations, that the tubules of the Wolffian body developed as outgrowths from the duct, and that the Malpighian bodies arose independently in the adjoining mesoblast. The views

---

[1] 'Monograph on the Development of Elasmobranch Fishes.'

[2] 'Urogenitalsystem der Plagiostomen. Arbeiten,' vol. ii.

[3] 'Entwickelung der Wirbelthiere,' &c.

[4] 'Entwickelungsgeschichte der Wirbelthiere,' Leipzig, 1861.

[5] 'Eierstock und Ei,' 1870.

of other observers, before 1874, were identical with one or the other of these.

Since 1874 the work of Götte[1] and Spengel[2] on Amphibia, Kölliker[3] on Aves, Braun[4] on Lacertilia, and Fürbringer on Teleostei, Amphibia, and Aves[5] has shown that the excretory system of all these animals is developed on a type seen in its simplest form in Elasmobranchs.

Kölliker first discovered in Aves structures composed of strings of cells connected with the Wolffian duct and peritoneal epithelium, and placed just ventral and internal to the former. These he compared to the early segmental tubes described in Elasmobranchs. From the similarity of these structures to those seen in Elasmobranchs and from his own observations he was led to assert for them a development similar to that described for Elasmobranchs, viz. from segmental involutions of the body-cavity epithelium.

In this he was followed by Fürbringer,[6] except in a small detail, the latter observer denying that these cell strings had any lumen opening into the body-cavity.

So far as I know, no ideas as to the morphological meaning of the Amniote kidney were held before 1874.

Conflicting statements were then put forward by different observers with regard to the actual embryonic development. Remak[7] and Kölliker[8] maintained that the whole of the epithelium of the kidney tubules, including that of the collecting and secreting tubules and the Malpighian bodies, was derived from a simple outgrowth from the ureter.

The condensed mesoblast tissue which lies near the ureter and its offshoots, in their opinion, only gives rise to the connective and vascular elements of the kidney.

Kölliker has expressed this view in the second edition of his great work on the development of Vertebrates. Löwe[9] has also recently arrived at the same conclusion from his observations on Mammals.

---

[1] 'Entwickelungsgesch. d. Unke.'

[2] "Das Urogen. system d. Amphibien," 'Arb. a. d. Zool. Inst.' Wurzburg, Bd. 3, 1876.

[3] 'Ent. gesch. d. Menschen u. d. höheren Thiere.'

[4] "Das Urogen-system d. d. Einheimischen Reptilien,' Semper's 'Arbeiten,' Bd. 4.

[5] "Zur vergleichenden Anat. u. Entwickelungsgeschichte d. Excretionsorgane der Vertebraten," 'Morphol. Jahrbuch,' Bd. 4. The reader is referred to this admirable essay for the literature, and a complete account of our knowledge of the excretory organs of Vertebrates.

[6] Loc. cit.

[7] 'Entwickelung der Wirbelthiere.'

[8] Loc. cit.

[9] 'Centralblatt für die Med. Wissenschaften,' Oct., 1879.

Kupffer,[1] Bornhaupt,[2] and Braun,[3] on the other hand, assert that the secretory tubules and Malpighian bodies are formed independently of the ureter in the condensed mesoblast tissue mentioned above, the outgrowths from the ureter merely giving rise to the collecting tubules.

I shall return, when I have described the kidney development in the chick, to a consideration and discussion of the various hypotheses which have been held concerning the Amniote kidney.

Development of Wolffian body.—The ages of the younger embryos from which the sections figured in the accompanying plates (VI and VII) were taken are indicated by the number of protovertebræ. In the older embryos this was not possible. In most cases the place in the body, from which a section figured was taken, is indicated by the number of the segment[4] in which it occurred, counting the first segment behind the auditory involutions as the first.

These determinations have been made with some care by mounting all the sections in order, and then by observing the protovertebræ, arranging them into groups corresponding to each protovertebra, beginning the process always in front.

The observations here recorded do not extend to any part of the Wolffian body in front of the fourteenth segment, nor to the development of the Wolffian duct. I have made some observations on both these parts, but they are not yet sufficiently complete to enable me to understand certain remarkable appearances in their development. The Wolffian body, like most other organs, develops first of all in front and then gradually backwards, so that supposing the development behind were the same as in front, the process might be shown by a series of sections from a single chick of the proper age. But this is not the case. In the chick the development of the Wolffian tubules behind is very different to that in front. This fact has apparently been overlooked by the most recent observers.

The development of the Wolffian body in the duck is much more completely similar throughout than in the chick, and reference will be at first made to figs. 2—5, taken from a duck embryo with thirty-one or thirty-two protovertebræ, in the following description.

[1] 'Arch. f. Mic. Anat.,' Bd. 1.

[2] 'Untersuchungen über d. Entwick. des Urogen. systems beim Hühnchen,' Diss. Inaug., Riga, 1867.

[3] Loc. cit.

[4] The term segment is used as equivalent to protovertebra, muscle plate.

The tubules of the Wolffian body do not develop from serial involutions of the peritoneal epithelium, but from the cells of the intermediate cell mass. The intermediate cell mass is so familiar to all students of Avian embryology that

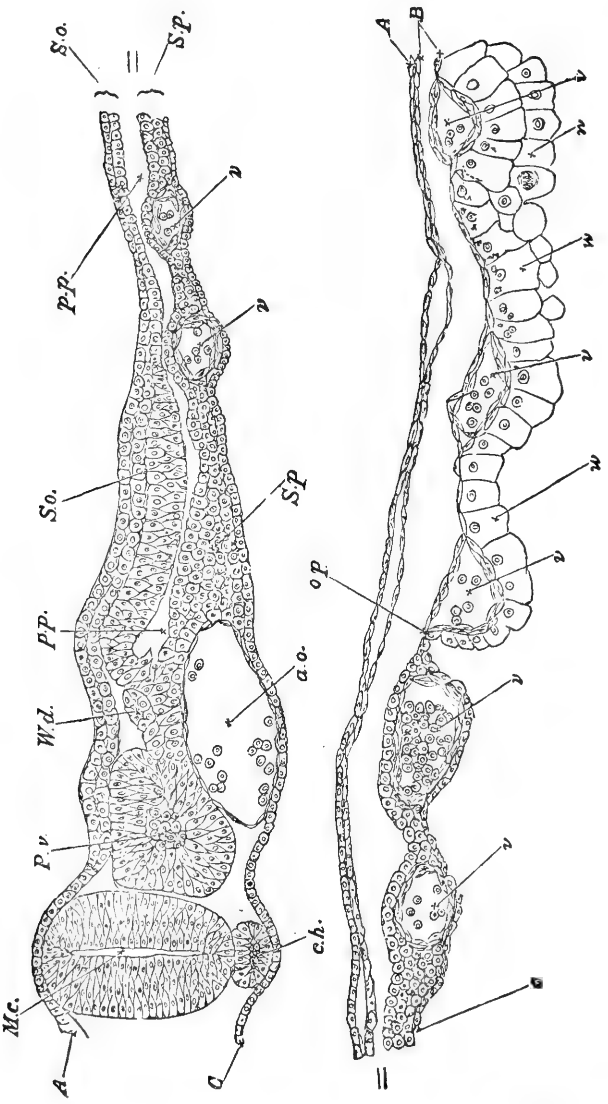


FIG. 1.[1]—Section from a chick of the second day, showing the intermediate cell-mass. *M. c.* Medullary canal. *P. v.* Protovertebra. *W. d.* Wolffian duct. *p. p.* Body-cavity. *c. h.* Notochord. *a. o.* aorta.

---

[1] For the woodcuts, figs. 1 and 2, I have to thank Mr. Balfour. Fig. 1 is from the 'Elements of Embryology.'

it is hardly necessary to say anything about it. It is a mass of cells[1] (woodcut, fig. 1), stretching between the protovertebra (*P. v.*) and the dorsal inner angle of the body-cavity (*p.p.*). It is on its first formation continuous with the peritoneal epithelium. Its relation to the protovertebra is obscure, and I have been unable, so far, to make it out satisfactorily. There is one point, however, to be borne in mind concerning this intermediate cell mass; it is continuous, *i. e.* is not divided by the lines of segmentation into areas corresponding to each protovertebra.

Very soon after the intermediate cell mass is established it undergoes a change. It becomes at some points more distinctly continuous with the peritoneal epithelium, at others less so. And finally this culminates in a clear continuity, as seen in fig. 2, and a marked discontinuity, as seen in fig. 3. In fig. 2 we have what practically amounts to a continuation of the body-cavity into the intermediate cell mass (*i c m.*); in fig. 3, on the other hand, the intermediate cell mass is distinctly disconnected with the peritoneal epithelium, and lies as a mass of cells between it and the protovertebra. Although these figures are not taken from contiguous sections, fig. 2 being taken from the thirtieth segment, and fig. 3 from the twenty-ninth, yet for all the important details fig. 3 represents exactly a section next or next but one to fig. 2. The intermediate cell mass is then now present as a cord of cells continuous from segment to segment, and continuous at intervals with the peritoneal epithelium. Fig. 4 represents the two conditions of the intermediate cell mass, as seen in a single section taken from the twenty-sixth segment.

At the next stage of development the intermediate cell mass entirely breaks away from the peritoneal epithelium, and lies as a cellular blastema just internal to the Wolffian duct. It may be called the Wolffian blastema.

The Wolffian blastema almost directly breaks up into the structures constituting the first rudiments of the Wolffian tubules (fig. 5).

The development of the Wolffian blastema in the chick needs further description.

In the anterior region of the Wolffian body, as far back as the nineteenth or twentieth segments, the above description of the conversion of the intermediate cell mass into the

---

[1] The term intermediate cell mass in this account is only used to indicate the cell mass connecting a *protovertebra* with the peritoneal epithelium, and never refers to the cell mass occupying the same position before segmentation has given rise to protovertebræ.

Wolffian blastema applies (*vide* fig. 1); but behind this region the development is different.

Here, even before the segments are formed, it is found that the cell mass, which on segmentation gives rise to the intermediate cell mass, is distinctly separate from the thick epithelium of the body-cavity, but attached to the cell mass, which will give rise to the protovertebra (fig. 6, taken from a chick with twenty-six protovertebræ behind the last protovertebra).

And this separation is apparently retained through later development. The cell mass (*i c m′*, fig. 6), in the next stage (fig. 7, taken from twenty-ninth segment of a chick with twenty-nine protovertebræ) is obviously the Wolffian blastema which, in a still later stage (fig. 10, from the twenty-ninth segment of a chick with thirty-four), gives rise to the commencing Wolffian tubule.

The same fact may be seen by comparing figs. 8 and 9, fig. 8 being taken from the twenty-fourth segment of a chick with twenty-six, and fig. 9 from the twenty-fourth segment of a chick with twenty-nine.

It will be observed, by inspection of figs. 6, 7, 8, that the peritoneal epithelium which adjoins the Wolffian blastema is thick, as it is elsewhere; while later (figs. 9, 10) it is in the same spot thin, as it is, or will be, in most other parts of the body-cavity.

No doubt this thick epithelium does, in the process of becoming thin, bud off cells, which travel inwards, and some of which may help to form the definite Wolffian blastema (figs. 9, 10). But this process takes place everywhere. In fact, at an early stage of development almost all the mesoblast cells are represented by the thick lining of the body-cavity; and it is by a process of growth inwards of cells from this that most of the connective tissue, &c., of the wall of the body and gut is derived; and, therefore, from the analogy of the fate of the cells growing out from the body-cavity wall in other places, we might fairly assume that those growing out from that particular part adjoining the intermediate cell mass or Wolffian blastema give rise, not to the Wolffian tubules, but to the connective tissue and blood-vessels of the Wolffian body. This is rendered highly probable from a consideration of some observations I have made on the development of the segmental tubes in Elasmobranchs, which point to the conclusion that the epithelial lining is derived from the cells of the intermediate cell mass. However that may be, of one fact there can be no doubt, viz. the cells from which the Wolffian tubules develop are not derived from serial ingrowths of the body-cavity epithelium, for this thinning of the peritoneal epithelium, adjoining the region where they will appear, is continuous, *i. e.* cells must grow in along a line extending the whole length of that part of the body-cavity which the Wolffian body adjoins.

The development of the Wolffian blastema, so described, is continued as far back as the opening of the Wolffian duct into the cloaca, which occurs in the thirty-fourth segment. In fig. 12 it may be seen in the thirty-second segment (*k b*).

The Wolffian blastema of the chick then develops in two slightly different ways.

In the anterior part, about as far back as the twentieth (fig. 1) segment, that process of development which has been described at length in the case of the duck (in which animal it is apparently the only method of development) is passed through in the chick.

Posteriorly from the twentieth segment the intermediate cell mass has never any connection with the peritoneal epithelium, and gives rise to the Wolffian blastema quite independently of the peritoneal epithelium. This latter process is clearly an abbreviation of that which takes place throughout in the duck and in the anterior part of the chick.

I have mentioned the twentieth segment as *about* the limit between the two. I cannot fix the exact limit.

It has been stated above that in the case of the duck and the anterior part of the chick (figs. 1, 2, 4) the intermediate cell mass becomes, at certain points, very markedly continuous with the peritoneal epithelium, and appears to enclose a prolongation of the body-cavity (fig. 1 and fig. 2). Such connections are undoubtedly rudiments of the nephrostomata seen in other Vertebrates. They do not occur segmentally, being situated as often as not between the protovertebræ.

Rudiments of these rudimentary nephrostomata occur in the posterior part of the chick's Wolffian body; that is, although a fairly sharp line can always be drawn between the Wolffian blastema and the peritoneal epithelium, yet the cells of the latter, at certain points, arrange themselves just as they do in front, where the line of the body-cavity is continued into the intermediate cell mass. These latter rudiments are very obscure, and I have been unable to make any satisfactory determination of their number. They may be due merely to an accidental arrangement of the cells, which might occur in consequence of the bend in the peritoneal epithelium at this point. Whether the rudimentary nephrostomata in the anterior part of the chick's kidney (fig. 1[1]) are continued as small channels in the intermediate cell mass or Wolffian blastema, and remain, enlarging when the Wolffian tubules are formed later, I have been unable to ascertain. Neither have I been able to satisfy myself as to another interesting point, viz. do those rudimentary nephrostomata correspond to the Wolffian tubules subsequently developed? In the chick's twentieth segment never more than three nephrostomata can, at the most, be made out, yet there are four or five primary Wolffian tubules later.

Has this increase been caused by the development of more tubules than there were nephrosomata, *i. e.* by intercalation, or has it been caused by a change in the relation of the parts to one another, due either to an elongation of the protovertebra or to the travelling forward of the tubules as they are developed behind?

I shall return to the consideration of this point in a future paper.

The mode in which the Wolffian blastema behind the twentieth[2] segment breaks up into tubules, so far as I have been able to ascertain it, is the following:—A number of vesicles, either oval or circular, lined by columnar cells, and lying just internal to the Wolffian duct, make their appearance (fig. 5). In longitudinal sections it may be seen that these vesicles closely adjoin one another antero-posteriorly. They are developed from those cells of the Wolffian blastema immediately adjoining the inner border of the Wolffian duct. By a study of transverse sections it appears that each vesicle is continuous ventrally with that part of the Wolffian blastema which has not undergone conversion into the walls of the vesicle, and which lies just internal to the vesicle. The cells of this part of the Wolffian blastema very soon arrange themselves round what appears as a continuation of the original vesicle (fig. 11). From the inner and dorsal wall of the last-formed structure a glomerulus is ultimately developed. The whole structure grows enormously, and gives rise to the Malpighian body and complicated coils of the later Wolffian tubule. At about the stage of development represented in fig. 11 the tubules acquire an opening into the Wolffian duct.

The question as to whether or no there are outgrowths from the Wolffian duct to meet the independently developed

---

[1] *Vide* also fig. 125, of Kölliker's 'Entwick. gesch. der Menschen u. der. h. Thiere.'

[2] I reserve an account of the development of the tubules in front of the twentieth segment, as my observations on this point are not yet sufficiently complete to enable me to speak with certainty.

Wolffian tubules is not easy to answer. I leave it open now, but hope to be in a position to give a definite answer soon. Now I will merely state that there are appearances in my sections which incline me to the opinion that there are outgrowths from the Wolffian duct which, in the case of the primary Wolffian tubules, are solid, but hollow in the case of the secondary and tertiary tubules.

The above description of the development of the primary Wolffian tubules differs from the most recent account of Kölliker[1] and Fürbringer.[2] I have stated above the views which these distinguished observers hold as to the development. They have described perfectly correctly one stage in the development of the anterior part of the Wolffian body. I have often seen the appearances given by Kölliker in fig. 125 of his work, and have given myself a similar representation (fig. 1). But if I understand them correctly they have given an erroneous account of the earlier development of these structures. Fürbringer says of them (p. 67): "Sie finden sich in reihenweiser Anordnung als solide Urnierenstränge die von dem parietalen Peritoneum ventral und medial vom Wolff'schen Gange ausgehen. . . . Sehr bald lösen sich diese Urnierenstränge von dem parietalen Peritoneum ab und liegen nun als rundliche solide Zellenmassen retroperitoneal neben dem Wolff'schen Gange, ein Stadium das die Beobachtungen der meisten Autoren deckt." It is easy to see how Fürbringer has been misled. He has seen in transverse sections in a fairly young chick the S-shaped strings of cells (solide Urnierenstränge) in connection with the peritoneal epithelium. He has also seen in an older chick the Wolffian blastema of the posterior region of the Wolffian body (rundliche solide Zellenmassen). Both these observations I can entirely confirm. But apparently he has not examined the condition of these structures at an earlier stage, assuming that they originate as solid outgrowths of the peritoneal epithelium. This assumption my observations prove to be unwarranted.

The older observers (see above) were quite correct in their statements of the origin of the Wolffian tubules, as structures developed in the intermediate cell mass, independently of the Wolffian duct, and later acquiring an opening into it.

Waldeyer's[3] statement that the Malpighian body thu develops, the rest of the Wolffian tubule developing as outgrowths from the Wolffian duct, is in my opinion erroneous. For if there be an outgrowth from the Wolffian duct it does not give rise to the whole tubule, exclusive of the

---

[1] Loc. cit.

[2] 'Morph. Jahrbuch,' Bd. 4.

[3] Loc cit.

Malpighian body, the structure developed independently in the intermediate cell mass certainly giving rise to more than the Malpighian body.

I now pass to the development of the secondary tubules, &c. Fürbringer[1] derives them also from peritoneal ingrowths. He has not, however, given, so far as I know, any figures showing this. I have examined this point with some care, but have quite failed to discover any traces of these secondary ingrowths.

The secondary tubules appear to me to arise from small masses of cells, which occupy, at a slightly earlier stage, the position of *wt.*^{2} in fig. 11. In this figure the vesicular rudiment of a secondary tubule has appeared in this mass of cells. The tertiary and quaternary, &c., tubules appear to arise successively at a slightly later stage from similar small masses of cells, which are always placed just dorsal to the last-formed tubule. The later development of these secondary, tertiary, &c., Wolffian tubules is very similar to that of the primary.

The time of development of the primary tubules relatively to that of the secondary, &c., tubules varies in different parts. Anteriorly the primary tubule is much more developed (in fact, has acquired an opening into the Wolffian duct), before the first trace of the secondary tubule arises, than posteriorly, where a secondary and tertiary tubule have appeared almost before the primary tubule has lost its vesicular structure (fig. 13).

The development of the secondary, &c., Wolffian tubules in the chick appears to be very much abbreviated.

Whatever may have been their development in phylogeny, no light is thrown upon it by their ontogeny. Nor even can a comparison be made between their development in the chick, and that in other forms in which it is possible to suppose the development is less abbreviated. In Elasmobranchs the secondary tubules, as Balfour[2] has shown, develop in connection with the Malpighian bodies of the primary tubules, as outgrowths from them, which eventually open into the collecting tubules of the segment in front. Neither Balfour nor, as far as I know, any other observer, have elucidated the development of the tertiary, &c., tubules in Elasmobranchs.

In the Salamander Fürbringer[3] has shown that they develop as they do in the chick from cell masses closely

---

[1] Loc. cit.

[2] Balfour, 'Elasmobranch Fishes.'

[3] Loc. cit.

adjoining the primary tubules, and from an inspection of his figures it is evident that these cell masses are situated close to the Malpighian body of the primary tubule. In the chick I have sought in vain for some clear sign in the development of these cells which would enable a comparison to be instituted with Elasmobranch development.

In the chick the cells of the Wolffian blastema do not all seem to be used in the formation of the primary tubule. Those, that are not, seem to collect at a special point, *i. e.* just dorsal to that part of the primary tubule which will become eventually the Malpighian body. The cells of the primary tubule are especially thick at this point, and perhaps they give rise to some of the cells for the secondary tubule (fig. 11). Even if this is the case—and we may look upon the secondary tubule as an outgrowth from the primary tubule—it is impossible to say where the secondary tubule so formed opens into the Wolffian duct.

This brings me to another difference between the dorsal tubules of the chick and those of Elasmobranchs. In the latter they all open into the collecting part of a primary Wolffian tubule. In the former they all open independently into the Wolffian duct, or it may be into an outgrowth from it, but separately from the primary tubule. This latter point I am, as above stated, obliged to leave open at present. The number of primary tubules present in one segment seems to be fairly constant, five or six to each segment, throughout the Wolffian body, except quite in front, where there seem to be fewer. All segments, from the twentieth to the thirtieth inclusive, contain five or six primary tubules. In front of the twentieth segment they seem gradually to decrease. In the first segment in which a fully developed tubule appears there seems only to be one, the number increasing rapidly to the twentieth.

The dorsal tubules appear in greater number behind than in front. In the twenty-eighth segment I have counted as many as four, but more are possibly developed later. They correspond in number to the primary tubules, *i. e.* if there are five primary tubules in the twenty-eighth segment, there are twenty secondary tubules (five sets of four). The most anterior segment in which a secondary tubule appears is the twenty-first or twenty-second; I have not been able, however, to localise it exactly.

Development of kidney.—The development of the Wolffian blastema from the intermediate cell mass has been described as far back as the thirty-fourth segment; *i. e.* to the opening of the Wolffian duct into the cloaca; it is never seen behind this point. But it does not all undergo the above development into Wolffian tubules. It breaks up into Wolffian tubules as far back as the thirtieth segment. Behind this point, *i. e.* from the thirty-first to the thirty-fourth segments inclusively, the Wolffian blastema undergoes quite a different fate. It remains for some time almost quite passive and ultimately gives rise to the epithelium of the permanent kidneys. In consequence of this I have called that part of the Wolffian blastema between the thirty-first and thirty-fourth segments the kidney blastema; and in future shall refer to it by that name (figs. 12, 15, 16, 17, *kb*). It is important to notice that this kidney blastema develops in an exactly similar manner to the Wolffian blastema.

It is not until well into the fourth day, when the ureter has appeared, that it is possible to draw the line between the two.

Fig. 12 is taken from the thirty-second segment of a chick with thirty-four protovertebræ; it shows a blastema of cells lying just internal to the Wolffian duct. Fig. 10 is taken from the twenty-ninth segment of the same chick. It shows the hindermost trace of a Wolffian tubule I could find at this stage. In all the sections between figs. 10 and 12 there is present, just as in fig. 12, a blastema of cells lying just internal to the Wolffian duct.

In a slightly older embryo the hindermost trace of a Wolffian tubule would be in the thirtieth segment. In still older embryos secondary tubules would have appeared in the thirtieth segment, but no trace of a primary tubule in the thirty-first, and so on in later stages, Wolffian tubules never appearing in the thirty-first segment. In the embryo, from which figs. 13 to 17 were taken, the ureter had not appeared. In examining a series of sections from the posterior part of this embryo, some of which are figured (figs. 13 to 17), the following points are noticeable, illustrating what has just been stated.

A primary and secondary tubule are present in fig. 14, and it is almost the last section in which any trace of a Wolffian tubule can be seen (the two above tubules are cut in the next two sections). The tubules adjacent anteriorly to these are three in number (fig. 13), consisting of primary, secondary, and tertiary. Supposing the Wolffian body were going on developing in the region behind that from which fig. 14 was taken, we ought at the least to find at this stage primary tubules in that region, for the formation of primary and secondary tubules is always separated by an interval of time. But no such primary tubules are seen. Behind fig. 14 (figs.

15 to 17) a blastema of cells is still present, precisely similar in its appearance and position with regard to the Wolffian duct to the Wolffian blastema seen anteriorly at earlier stages, and to the blastema seen in the same region at later stages (fig. 12). And this can be traced back to the opening of the Wolffian duct into the cloaca (fig. 17).

To this blastema of cells I have given the name kidney blastema; it is at this stage perfectly continuous anteriorly with the hinder Wolffian tubules, the junction between the two lying in one of the two sections intervening between figs. 14 and 15. I ought rather to say the line of future separation, for so far they have been always continuous, having developed so. The continuity between the kidney blastema (*kb*) and the hinder part of the Wolffian body may be seen in fig. 21, which is taken from a chick of nearly the same age as that from which figs. 13—17 were.

In this figure the section has passed through the hind end of the Wolffian duct and through the kidney blastema, and has just shaved the hinder end of the Wolffian body, in consequence of which the hinder Wolffian tubules are only indistinctly visible.

The next change to notice is caused by the appearance of the ureter. It arises as a growth forward from the dorsal border of the enlarged end of the Wolffian duct. This has been generally recognised since Kupffer's[1] account. The dilatation of the hind end of the Wolffian duct occurs in a very slightly later embryo than that from which fig. 21 was taken.

The kidney blastema is now found not ventrally close to the body-cavity, but lies dorsal to its former position, just internal to the dorsal extremity of the dilated Wolffian duct (fig. 20). From this dilatation there grows forward a duct, the ureter (fig. 19), on the inner side of which lies the kidney blastema.

The ureter, at this stage, has not a very great extent, and is only seen for a few more sections; in fig. 18, still behind the Wolffian body, the ureter is not visible; but the kidney blastema occupies a dorsal position, as it did in the posterior section in which the ureter was present (fig. 19).

In tracing it forward it gradually descends and becomes continuous with the hind end of the Wolffian body.

In yet older embryos, in which the ureter is more developed and overlaps the hind end of the Wolffian body, the kidney blastema has quite broken off from the Wolffian body, and invests the anterior end of the ureter, so that in a series of transverse sections through a chick at this age we should see

---

[1] 'Arch. f. M. Anat.,' Bd. 2.

posteriorly, in the same section with the now complicated Wolffian body, a dorsal mass of cells. Gradually travelling backwards a duct would appear cut across lying in the mass of cells; further back still we should see no Wolffian body, but merely a duct with a mass of cells lying just internal to it, placed well dorsal to the Wolffian duct. This mass of cells is the kidney blastema; and the duct is the ureter.

Such would be seen in a chick at the end of the fifth day.

On the sixth day the ureter grows in length, the kidney blastema accompanying it, and enveloping its anterior extremity.

The ureter now dilates at intervals, and the kidney blastema especially collects round these dilatations. From the latter, the number of which I have not determined, the kidney tubules grow out. In a chick of the seventh day the tubules are just beginning to grow out from these dilatations. The two posterior tubules are, however, far more advanced than the anterior.

The ureter is now a small duct lying just dorsal to the Wolffian body; except at its anterior extremity, where it is rather more dorsal, and is completely surrounded by the kidney blastema.

Almost immediately in front of the hind end of the ureter a tubule is given off, which runs dorsalwards and outwards. The kidney blastema no longer adjoins the ureter, but is disposed round the branches of this tubule. The ureter is continued forwards through a considerable number of sections, giving off no tubules, and unaccompanied by the kidney blastema. It then becomes continuous with a tubule, which has already been visible in many sections surrounded by kidney blastema, and which, though not so much branched as the posterior tubule above mentioned, is more developed than any tubule met with in front.

The ureter continues as a small duct lying just dorsal to the Wolffian body.

In this embryo (seventh day), travelling forwards, several dilatations could be made out. The appearance presented by such a dilatation in transverse section and its position with regard to the Wolffian body, may be gathered from an inspection of fig. 22.

In this section the lateral walls of the dorsal part of the dilatation of the ureter are closely applied, the lumen being very indistinct.

Around the dorsal part of the dilatation the kidney blastema is present.

In the next section, or in the next section but one (fig. 23), either backwards or forwards, the dorsal dilatation would be no longer visible, but, occupying the position of the dorsal part of the dilatation, would be seen a tubule surrounded by the cells of the kidney blastema.

In the next section to this (fig. 24) the walls of the tubule become indistinctly marked off from the kidney blastema. Some of the large columnar cells of the kidney tubule become branched, the processes being continuous with the processes of the branched cells of the kidney blastema. In fact, every stage of cell shape between a columnar lining cell of the tubule and a branched cell of the blastema is visible.

The lumen of the tubule is no longer distinct, it not being possible to say what is an intercellular space and what the lumen of the tubule.

In the next section no trace of a tubule is visible, its place being occupied by the cells of the blastema.

Fig. 23 is taken from a section next but one to fig. 22. Nine such dorsal dilatations of the ureter, with commencing tubules growing from them, could be made out in the embryo under consideration.

In front of the anterior dilatation the tubules open directly into the ureter which in this region has become more dorsal with regard to the Wolffian body. Tubules in this region, moreover, are given off from the ventral side of the ureter, corresponding almost exactly to those given off from the dorsal side. Four pairs could be made out; after which the ureter ended closely surrounded on all sides by dense kidney blastema.

The next and last stage, which I have closely examined, was in an eight-day chick. The kidney had reached a great complication of structure. Malpighian bodies had, however, not distinctly appeared. The tubules were still surrounded by kidney blastema which was especially conspicuous at their growing ends. The appearance of the latter, which was exactly similar in all essential details to the growing points of the tubules of the stage last described, is represented in fig. 24.

Before considering the bearing of the above facts upon the questions asked at the outset, I will recapitulate the more important points in the development of the Avian kidney and Wolffian body.

1. The cells which give rise to the Wolffian and kidney tubules do not develop as involutions of the peritoneal epithelium, but from a blastema of cells derived from the intermediate cell mass.

2. The blastema of the kidney is at first perfectly continuous with that of the Wolffian body, and cannot be distinguished from it.

3. Wolffian tubules do not appear in any part of the blastema behind the thirtieth segment. Primary, secondary, and tertiary, &c., tubules are developed in that part of it placed in the thirtieth and anterior segments as far as the twenty-first or twenty-second, and primary tubules in yet anterior segments.

4. The blastema in the thirty-first to thirty-fourth segments, on the appearance of the ureter, moves dorsalwards from the Wolffian duct, breaking away from the hindermost Wolffian tubules and enters into close relation with the ureter.

5. This part of the blastema—the kidney blastema—especially collects round swellings on the ureter, from which kidney tubules grow out.

6. These kidney tubules burrow into the kidney blastema, their growing points being continuous with the cells of the blastema.

Five years ago Balfour [1] and Semper [2] independently put forward the hypothesis that the kidney of the Amniota holds the same relation to the embryonic Wolffian body as does the adult kidney in Elasmobranchs.

Balfour wrote then:[3] "The last feature in the anatomy of the Selachians which requires notice is the division of the kidney into two portions, an anterior and posterior. The anatomical similarity between this arrangement and that of higher Vertebrates (birds, &c.) is very striking. The anterior one precisely corresponds, anatomically, to the *Wolffian body*, and the posterior to the true permanent *kidney* of higher Vertebrates; and when we find that in the Selachians the duct for the anterior serves also for the semen, as does the duct of higher Vertebrates, this similarity seems almost to amount to identity."

The development of the kidney of the bird has never been fully worked out, so that this hypothesis, arrived at from a consideration of the facts of comparative anatomy and Elasmobranch embryology, has hitherto not been tested by the facts of Avian embryology. The observations described above were undertaken with a view of testing this hypothesis, and, in my opinion, it has fully stood the test.

The development of the kidney in the chick points most decidedly to the conclusion that it is merely the posterior part of the Wolffian body—or, perhaps, it would be better to say, of a primitive organ, the anterior part of which is now

---

[1] "Urogenital Organs of Vertebrates," 'Journal of Anatomy and Physiology,' vol. x.

[2] Loc. cit.

[3] P. 27.

seen as the Wolffian body—the whole of this primitive organ in Elasmobranch embryos being termed Wolffian body.

The most important fact in favour of Balfour's hypothesis is the primitive continuity in early stages in the bird of the cells from which both Wolffian body and kidney arise.

The differences in later development cannot be looked upon as a serious difficulty when we remember the immense differences which many undoubtedly homologous organs show in their embryonic development in various animals.

It has been stated (see above, p. 64) by many students of Avian embryology that the kidney tubules develop as outgrowths from the ureter, and that the cells of the kidney blastema merely give rise to the vascular elements of the glomerulus. This view, whether considered *à priori,* or with reference to the facts of development, cannot for a moment be maintained.

If Balfour's hypothesis as to the relation of the kidney to the Wolffian body be accepted, and I do not see how it can be rejected, assuming the truth of the facts of development recorded in this account, it would require very strong proof indeed to establish the fact that the cells of the kidney blastema give rise merely to the vascular elements of the glomerulus, and take no part in the formation of the secretory epithelium of the kidney tubules, such as is taken in the formation of tubules of a very similar organ by cells developed in a precisely similar way. Such proof is not forthcoming, and would be very hard to give.

Considering the very late development of the posterior part of the Wolffian body (kidney) in the chick with reference to that of the anterior part, it surely cannot be a matter of surprise if the development has been modified, the walls of the tubule arising from the cells of the blastema; the lumen, however, not as in the anterior part, first appearing as an independent cavity, which opens later into the duct, but being from the first continuous with the lumen of the ureter.

Fürbringer's suggestion, that the Amniote kidney is derived from dorsal tubules of the Wolffian body, is based mainly on the fact that it lies dorsal to the Wolffian body, and an observation of Braun's for Lizards. Braun has stated for these animals that the kidney blastema develops from irregular ingrowths of the peritoneal epithelium, at a period when the secondary dorsal tubules of the Wolffian body are developing.

With regard to the first point it is to be noted that the dorsal position of the kidney is clearly a secondary change, appearing only late in development, and due obviously to the great size the kidney attains. Moreover, according to Fürbringer's view, one would expect to find some kind of continuity between the developing kidney and dorsal part of the Wolffian body; but no trace of any such connection can ever be seen.

Finally, in view of the facts of development here recorded for the chick, and of those about to be mentioned for Elasmobranchs, Braun's observations on the development of the kidney blastema of Lizards from peritoneal ingrowths cannot be accepted without further evidence. The irregularly scattered cells lying between the Wolffian duct and the peritoneal epithelium, which Braun has figured, are by no means proof of ingrowth of cells from the peritoneal epithelium. Such an irregular arrangement of cells can be seen anywhere adjoining the body-cavity epithelium.

Kölliker's view that the kidney of the Amniota is an organ *sui generis*, which was not present in any form in the excretory system of the common ancestor of Icthyopsida and Amniota, needs in my opinion no refutation; for if true it can only be established by proving all other hypotheses concerning the kidney to be untenable.

Development of segmental tubes in Elasmobranchii.—I should hardly have been bold enough to publish these observations on the development of the chick's Wolffian body, opposed as they are to statements supported by great authority, had I not had the opportunity of examining the early development of the parts in question in Elasmobranchs. I was thus enabled to confirm suspicions which I had entertained since examining the development of the Wolffian body of birds, as to the correctness of the description of the earliest stages in these fishes. It is well known that the Wolffian tubules of Elasmobranchii are derived from the segmentally-arranged segmental tubes. These latter were said to arise by an invagination, at first solid but subsequently becoming hollow, of the peritoneal epithelium just internal to the segmental duct into the cells of the intermediate cell mass. The intermediate cell mass was said to be produced by the coming together of the splanchnic and somatic layers of that part of the body cavity, which at an earlier period existed connecting the general ventral body cavity with the dorsal continuations of it in the muscle plates.

On examining specimens of young Elasmobranch (Scyllium, Pristiurus, Torpedo) embryos, I found that the passage connecting the general body-cavity with that in the muscle-plates persisted later than had been described. Its connection with the ventral dilatation of the muscle-plate cavity is carried ventralwards as far as the outer dorsal corner of the segmental duct; so that it appears as a canal opening into the body-cavity just internal to the segmental duct, and thence curling round its dorsal wall to open into the muscle-plate cavity. The ventral outer wall of this passage is formed of large columnar cells, the inner and dorsal wall of much flatter cells (woodcut, fig. 2), as seen in transverse sections.

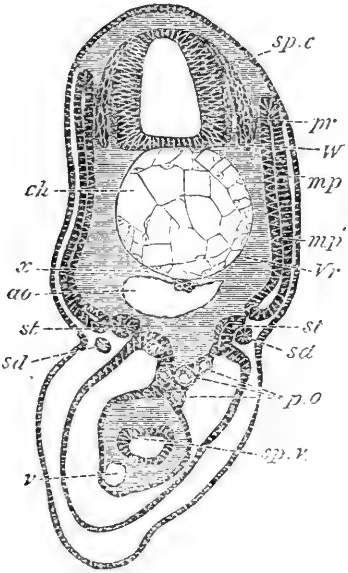


FIG. 2.[1]—Transverse section through a young embryo of Scyllium. *mp.* Muscle-plate. *st.* Segmental tube. *sd.* Segmental duct. *ch.* Notochord. *sp. v.* Alimentary canal.

At the next stage of development the passage becomes quite separated from the muscle-plate cavity, and now lies as a blind tube, opening into the body-cavity internal to the segmental duct, its blind outer end being applied to the ventral dilatation of the muscle-plate body-cavity (woodcut, fig. 2). This blind tube is the commencement of a segmental tube.

I have traced it through a series of older embryos to the fully-formed segmental tube. The adjoining woodcut (fig. 2)

---

[1] Fig. 2 is from Mr. Balfour's forthcoming treatise on 'Comparative Embryology.' It is copied from a figure in his 'Monograph on the Development of Elasmobranch Fishes.'

represents a section from a Scyllium embryo, in which the segmental tube has just broken away from the muscle plate; in a slightly younger embryo, or perhaps in posterior sections of the same embryo, the cavity of the segmental tube (*st*) would communicate with the ventral dilatation of the muscle plate (*mp*), at the point where they are in contact in the figure.

This mode of origin of the segmental tubes of Elasmobranchii renders the origin of the same structures in the chick less extraordinary than it at first sight seemed.

I refrain now from the discussions and perhaps hypotheses which this observation on the development of the Elasmobranch segmental tubes suggests. On one point, however, there can be little doubt, viz. that segmental involutions of the peritoneal epithelium which have been described in the Teleostei, Amphibia, Ganoids, Mammals, will have to be given up. At any rate the current statement on this point cannot be accepted without further proof.

I have made observations on the Teleostei and Sturgeon (Mr. Balfour having kindly put his specimens at my disposal) which tend to show, not, however, with certainty, that in the embryos of these forms at any rate there are no serial involutions of the body-cavity epithelium to form the segmental tubes. The method of development in these forms appears to me to be very much modified, if we continue to regard the development in Elasmobranchs as primitive.

The Wolffian body in all those animals whose ova have a relatively small food yolk seems to be retarded in development; while the head kidney, the relation of which to the rest of the excretory system is not understood, attains an early development and functions as the larval excretory organ. Very possibly a clue to the explanation of the retardation in the development of the Wolffian body and of the morphological meaning of the head kidney, in Teleostei, Amphibia, &c., may be obtained by a consideration of this coincidence and others hitherto apparently overlooked.

I hope in another paper to discuss these questions and some others which have been passed over here, and to describe the development of the anterior part of the Wolffian body in the chick.

In conclusion, I wish to acknowledge the great obligations I am under to Mr. Balfour. Not only have I to thank him for his kindness in placing all his preparations and specimens at my disposal, but, for what has been far more valuable, the help and encouragement he has given me through the whole course of this investigation.

NOTES *on the* DEVELOPMENT *of the* ARANEINA. By F. M. BALFOUR, M.A., F.R.S., Fellow of Trinity College, Cambridge. With Plates VIII, IX, and X.

THE following observations do not profess to contain a complete history of the development even of a single species of spider. They are the result of investigations carried on at intervals during rather more than two years, on the ova of *Angelena labyrinthica;* and I should not have published them now, if I had any hope of being able to complete them before the appearance of the work I am in the course of publishing on Comparative Embryology. It appeared to me, however, desirable to publish in full such parts of my observations as are completed before the appearance of my treatise, since the account of the development of the Araneina is mainly founded upon them.

My investigations on the germinal layers and organs have been chiefly conducted by means of sections. To prepare the embryos for sections, I employed the valuable method first made known by Bobretsky. I hardened the embryos in bichromate of potash, after placing them for a short time in nearly boiling water. They were stained as a whole with hematoxylin after the removal of the membranes, and embedded for cutting in coagulated albumen.

The number of investigators who have studied the development of spiders is inconsiderable. A list of them is given at the end of the paper.

The earliest writer on the subject is Herold (No. 4); he was followed after a very considerable interval of time by Claparède (No. 3), whose memoir is illustrated by a series of beautiful plates, and contains a very satisfactory account of the external features of development.

Balbiani (No. 1) has gone with some detail into the history of the early stages; and Ludwig (No. 5) has published some very important observations on the development of the blastoderm. Finally, Barrois (No. 2) has quite recently taken up the study of the group, and has added some valuable observations on the development of the germinal layers.

In addition to these papers on the true spiders, important investigations have been published by Metschnikoff on other groups of the Arachnida, notably the scorpion. Metschnikoff's observations on the formation of the germinal layers and organs accord in most points with my own.

The development of the Araneina may be divided into four periods: (1) the segmentation; (2) the period from the close of the segmentation up to the period when the segments of the body commence to be formed; (3) the period from the commencing formation of the segments to the development of the full number of limbs; (4) the subsequent stages up to the attainment of the adult form.

In my earliest stage the segmentation was already completed, and the embryo was formed of a single layer of large flattened cells enveloping a central mass of polygonal yolk-segments.

Each yolk-segment is formed of a number of large clear somewhat oval yolk-spherules. In hardened specimens the yolk-spherules become polygonal, and in ova treated with hot water prior to preservation are not unfrequently broken up. Amongst the yolk-segments are placed a fair number, of nucleated bodies of a very characteristic appearance. Each of them is formed of (1) a large, often angular, nucleus, filled with deeply staining bodies (nucleoli ?). (2) Of a layer of protoplasm surrounding the nucleus, prolonged into a protoplasmic reticulum. The exact relation of these nucleated bodies to the yolk-segments is not very easy to make out, but the general tendency of my observations is to show (1) that each nucleated body belongs to a yolk-sphere, and (2) that it is generally placed not at the centre, but to one side of a yolk-sphere. If the above conclusions are correct each complete yolk-segment is a cell, and each such cell consists of a normal nucleus, protoplasm, and yolk-spherules. There is a special layer of protoplasm surrounding the nucleus, while the remainder of the protoplasm consists of a reticulum holding together the yolk-spherules. Yolk-cells of this character are seen in Pl. IX and X, figs. 10—21.

The nuclei of the yolk-cells are probably derived by division from the nuclei of the segmentation rosettes (*vide* Ludwig, No. 5), and it is probable that they take their origin at the time when the superficial layer of protoplasm separates from the yolk-columns below to form the blastoderm.

The protoplasm of the yolk-cells undergoes rapid division, as is shewn by the fact that there are often two nucleated bodies close together, and sometimes two nuclei in a single mass of protoplasm (fig. 10). It is probable that in some cases the yolk-spheres divide at the same time as the protoplasm belonging to them; the division of the nucleated bodies is, however, in the main destined to give rise to fresh cells which enter the blastoderm.

I have not elucidated to my complete satisfaction the next stage or two in the development of the embryo; and have not succeeded in completely reconciling the results of my own observations with those of Claparède and Balbiani. In order to show exactly where my difficulties lie it is necessary briefly to state the results arrived at by the above authors.

According to Claparède the first differentiation in Pholcus consists in the accumulation of the cells over a small area to form a protuberance, which he calls the *primitive cumulus.* Owing to its smaller specific gravity the part of the ovum with the cumulus always turns upwards, like the blastodermic pole of a fowl's egg.

After a short time the cumulus elongates itself on one side, and becomes connected by a streak with a white patch, which appears on the surface of the egg, about 90° from the cumulus. This patch gradually enlarges, and soon covers the whole surface of the ovum except the region where the cumulus is placed. It becomes the ventral plate or germinal streak of the embryo, its extremity adjoining the cumulus is the anal extremity, and its opposite extremity the cephalic one. The cumulus itself is placed in a depression on the dorsal surface of the ovum. Claparède compares the cumulus to the dorsal organ of many Crustacea.

Balbiani (No. 1) describes the primitive cumulus in *Tegenaria domestica, Epeira diadema,* and *Agelena labyrinthica,* as originating as a protuberance at the centre of the ventral surface, surrounded by a specialised portion of the blastoderm (p. 57), which I will call the ventral plate. In *Tegenaria domestica* he finds that it encloses the so-called yolk-nucleus, p. 62. By an unequal growth of the ventral plate the primitive cumulus comes to be placed at the cephalic pole of the ventral plate. The cumulus now becomes less prominent, and in a few cases disappears. In the next stage the central part of the ventral plate becomes very prominent and forms the procephalic lobe, close to the anterior border of which is usually placed the primitive cumulus (p. 67). The space between the cumulus and the procephalic lobe grows larger, so that the latter gradually travels towards the dorsal surface and finally vanishes. Behind the procephalic lobe the first traces of the segments make their appearance, as three transverse bands, before a distinct anal lobe becomes apparent.

The points which require to be cleared up are, (1) what is the nature of the primitive cumulus? (2) where is it situated in relation to the embryo? Before attempting to answer these questions I will shortly describe the development, so far as I have made it out, for the stages during which the cumulus is visible.

The first change that I find in the embryo (when examined after it has been hardened)[1] is the appearance of a small, whitish spot, which is at first very indistinct. A section through such an ovum (Pl. IX, fig. 10) shows that the cells of about one half of the ovum have become more columnar than those of the other half, and that there is a point (*pr. c.*) near one end of the thickened half where the cells are more columnar, and about two layers or so deep. It appears to me probable that this point is the whitish spot visible in the hardened ovum. In a somewhat later stage (Pl. VIII, fig. 1) the whitish spot becomes more conspicuous (*pc*), and appears as a distinct prominence, which is, without doubt, the primitive cumulus, and from it there proceeds on one side a whitish streak. The prominence, as noticed by Claparède and Balbiani, is situated on the flatter side of the ovum. Sections at this stage show the same features as the previous stage, except that (1) the cells throughout are smaller, (2) those of the thickened hemisphere of the ovum more columnar, and (3) cumulus is formed of several rows of cells, though not divided into distinct layers. In the next stage the appearances from the surface are rather more obscure, and in some of my best specimens a coagulum, derived from the fluid surrounding the ovum, covers the most important part of the blastoderm. In Pl. VIII, fig. 2, I have attempted to represent, as truly as I could, the appearances presented by the ovum. There is a well-marked whitish side of the ovum, near one end of which is a prominence (*pc*), which must, no doubt, be identified with the cumulus of the earlier stages. Towards the opposite end, or perhaps rather nearer the centre of the white side of the ovum, is an imperfectly marked triangular white area. There can be no doubt that the line connecting the cumulus with the triangular area is the future long axis of the embryo, and the white area is, without doubt, the procephalic lobe of Balbiani.

A section of the ovum at this stage is represented in Pl. IX, fig. 11. It is not quite certain in what direction the section is taken, but very probably it is somewhat oblique to the long axis. However this may be, the section

---

[1] I was unfortunately too much engaged, at the time when the eggs were collected, to study them in the fresh condition; a fact which has added not a little to my difficulties in elucidating the obscure points in the early stages.

shows that the whitish hemisphere of the blastoderm is formed of columnar cells, for the most part two or so layers deep, but that there is, not very far from the middle line, a wedge-shaped internal thickening of the blastoderm where the cells are several rows deep. With what part visible in surface view this thickened portion corresponds is not clear. To my mind it most probably corresponds to the larger white patch, in which case I have not got a section through the terminal prominence. In the other sections of the same embryo the wedge-shaped thickening was not so marked, but it, nevertheless, extended through all the sections. It appears to me very possible that it constitutes a longitudinal thickened ridge of the blastoderm. In any case it is clear that the white hemisphere of the blastoderm is a thickened portion of the blastoderm, and that the thickening is in part due to the cells being more columnar, and, in part, to their being more than one row deep, *though they have not become divided into two distinct germinal layers.* It is further clear that the increase in the number of cells in the thickened part of the blastoderm is, *in the main, a result of the multiplication of the original single row of cells,* while a careful examination of my sections proves that it is also partly due to cells, derived from the yolk, having been added to the blastoderm.

In the following stage which I have obtained (which cannot be very much older than the previous stage, because my specimens of it come from the same batch of eggs), a distinct and fairly circumscribed thickening forming the ventral surface of the embryo has become established. Though its component parts are somewhat indistinct, it appears to consist of a procephalic lobe, a less prominent caudal lobe, and an intermediate portion divided into about three segments; but its constituents cannot be certainly identified with the structures visible in the previous stage. I am inclined, however, to identify the anterior thickened area of the previous stage with the procephalic lobe, and a slight protuberance of the caudal portion (visible from the surface) with the primitive cumulus. I have, however, failed to meet with any trace of the cumulus in my sections.

To this stage, which forms the first of the second period of the larval history, I shall return, but it is necessary now to go back to the observations of Claparède and Balbiani.

There can, in the first place, be but little doubt that what I have called the primitive cumulus in my description is the structure so named by Claparède and Balbiani.

It is clear that Balbiani and Claparède have both failed to appreciate the importance of this organ, which my observations show to be the part of the ventral thickening of the blastoderm where two rows of cells are first established, and therefore the point where the first traces of the future mesoblast become visible.

Though Claparède and Balbiani differ somewhat as to the position of the organ, they both make it last longer than I do: I feel certainly inclined to doubt whether Claparède is right in considering a body he figures after six segments are present, to be the same as the dorsal organ of the embryo before the formation of any segments, especially as all the stages between the two appear to have escaped him. In Agelena there is undoubtedly no organ in the position he gives when six segments are formed.

Balbiani's observations accord fairly with my own up to the stage represented in fig. 2. Beyond this stage my own observations are not satisfactory, but I must state that I feel doubtful whether Balbiani is correct in his description of the gradual separation of the procephalic lobe and the cumulus, and the passage of the latter to the dorsal surface, and think it possible that he may have made a mistake as to which side of the procephalic lobe, in relation to the parts of the embryo, the cumulus is placed.

Although there appear to be grounds for doubting whether either Balbiani and Claparède are correct in the position they assign to the cumulus, my observations scarcely warrant me in being very definite in my statements on this head, but, as already mentioned, I am inclined to place the organ near the posterior end (and therefore, as will be afterwards shown, in a somewhat dorsal situation) of the ventral embryonic thickening.

In my earliest stage of the third period there is present, as has already been stated, a procephalic lobe, and an indistinct and not very prominent caudal portion, and about three segments between the two. The definition of the parts of the blastoderm at this stage is still very imperfect, but from subsequent stages it appears to me probable that the first of the three segments is that of the first pair of ambulatory limbs, and that the segments of the cheliceræ and pedipalpi are formed later than those of the first three ambulatory appendages.

Balbiani believes that the segment of cheliceræ is formed later than the segments immediately behind it. He further concludes, from the fact that this segment is cut off from the procephalic portion in front, that it is really part of the procephalic lobe. I cannot accept the validity of this argument; though I am glad to find myself in, at any rate, partial harmony with the distinguished French embryologist as to the facts. Balbiani denies for this stage the existence of a caudal lobe. There is certainly, as is very well shown in my longitudinal sections, a thickening of the blastoderm in the caudal region, though it is not so prominent in surface views as the procephalic lobe.

A transverse section through an embryo at this stage (Pl. IX, fig. 12) shows that there is a ventral plate of somewhat columnar cells more than one row deep, and a dorsal portion of the blastoderm formed of a single row of flattened cells. Every section at this stage shows that the inner layer of cells of the ventral plate is receiving accessions of cells from the yolk, which has not to any appreciable extent altered its constitution. A large cell, passing from the yolk to the blastoderm, is shown in fig. 12 at *y. c.*

The cells of the ventral plate are now divided into two distinct layers. The outer of these is the *epiblast,* the inner the *mesoblast.* The cells of both layers are quite continuous across the median line, and exhibit no trace of a bilateral arrangement.

This stage is an interesting one on account of the striking similarity which (apart from the amnion) exists between a section through the blastoderm of a spider and that of an insect immediately after the formation of the mesoblast. The reader should compare Kowalevsky's ('Mem. Acad. Petersbourg,' vol. xvi, 1871) fig. 26, pl. ix with my fig. 12. The existence of a continuous ventral plate of mesoblast has been noticed by Barrois (p. 532), who states that the two mesoblastic bands originate from the longitudinal division of a primitive single band.

In a slightly later stage (Pl. VIII, fig. 3 *a* and 3 *b*) six distinct segments are interpellated between the procephalic and the caudal lobes. The two foremost, *ch* and *pd* (especially the first), of these are far less distinct than the remainder, and the first segment is very indistinctly separated from the procephalic lobe. From the indistinctness of the first two somites, I conclude that they are later formations than the four succeeding ones. The caudal and procephalic lobes are very similar in appearance, but the procephalic lobe is slightly the wider of the two. There is a slight protuberance on the caudal lobe, which is possibly the remnant of the cumulus. The superficial appearance of segmentation is produced by a series of transverse valleys, separating raised intermediate portions which form the segments. The ventral thickening of the embryo now occupies rather more than half the circumference of the ovum.

Transverse sections show that considerable changes have been effected in the constitution of the blastoderm. In the previous stage, the ventral plate was formed of an uniform external layer of epiblast, and a continuous internal layer of mesoblast. The mesoblast has now become divided along the whole length of the embryo, except, perhaps, the procephalic lobes, into two lateral bands which are not continuous across the middle line (Pl. IX, fig. 13 *me*). It has, moreover, become a much more definite layer, closely attached to the epiblast. Between each mesoblastic band and the adjoining yolk there are placed a few scattered cells, which in a somewhat later stage become the splanchnic mesoblast. These cells are derived from the yolk-cells; and almost every section contains examples of such cells in the act of joining the mesoblast..

The epiblast of the ventral plate has not, to any great extent, altered in constitution. It is, perhaps, a shade thinner in the median line than it is laterally. The division of the mesoblast plate into two bands, together, perhaps, with the slight reduction of the epiblast in the median ventral line, gives rise at this stage to an imperfectly marked median groove.

The dorsal epiblast is still formed of a single layer of flat cells. In the neighbourhood of this layer the yolk nuclei are especially concentrated. The yolk itself remains as before.

The segments continue to increase regularly, each fresh segment being added in the usual way between the last formed segment and the unsegmented caudal lobe. At the stage when about nine or ten segments have become established, the first rudiments of appendages become visible. At this period (Pl. VIII, fig. 4) there is a distinct median ventral groove, extending through the whole length of the embryo, which becomes, however, considerably shallower behind. The procephalic region is distinctly bilobed. The first segment (that of the cheliceræ) is better marked off from it than in the previous stage, but is without a trace of an appendage, and exhibits therefore, in respect to the development of its appendages, the same retardation that characterised its first appearance. The next five segments, viz. those of the pedipalpi and four ambulatory appendages, present a very well-marked swelling at each extremity. These swellings are the earliest traces of the appendages. Of the three succeeding segments, only the first is well differentiated. The caudal lobe, though less broad than the procephalic lobe, is still a widish structure. The most important internal changes concern the mesoblast, which is now imperfectly though distinctly divided into somites, corresponding with segments visible externally. Each mesoblastic somite is formed of a distinct somatic layer closely attached to the epiblast, and a thinner and less well-marked splanchnic layer. In the appendage-bearing segments the somatic layer is continued up into the appendages.

The epiblast is distinctly thinner in the median line than at the two sides.

The next stage figured (Pl. VIII, figs. 5 and 6) is an important one, as it is characterised by the establishment of the full number of appendages. The whole length of the ventral plate has greatly increased, so that it embraces nearly the circumference of the ovum, and there is left uncovered but a very small arc between the two extremities of the plate (Pl. VIII, fig. 6; Pl. IX, fig. 15). This arc is the future dorsal portion of the embryo, which lags in its development immensely behind the ventral portion.

There is a very distinctly bilobed procephalic region (*pr. l*) well separated from the segment with the cheliceræ (*ch*). It is marked by a shallow groove opening behind into a circular depression (*st.*)—the earliest rudiment of the stomodæum. The six segments behind the procephalic lobes are the six largest, and each of them bears two prominent appendages. They constitute the six appendage-bearing segments of the adult. The four future ambulatory appendages are equal in size: they are slightly larger than the pedipalpi, and these again than the cheliceræ. Behind the six somites with prominent appendages there are four well-marked somites, each with a small protuberance. These four protuberances are provisional appendages. They have been found in many other genera of Araneina (Claparède, Barrois). The segments behind these are rudimentary and difficult to count, but there are, at any rate, five, and at a slightly later stage probably six, including the anal lobe. These fresh segments have been formed by the continued segmentation of the anal lobe, which has greatly altered its shape in the process. The ventral groove of the earlier stage is still continued along the whole length of the ventral plate.

By the close of this stage the full number of post-cephalic segments has become established. They are best seen in the longitudinal section (Pl. IX, fig. 15). There are six anterior appendage-bearing segments, followed by four with rudimentary appendages (not seen in this figure), and six without appendages behind. There are, therefore, sixteen in all. This number accords with the result arrived at by Barrois, but is higher by two than that given by Claparède.

The germinal layers (*vide* Pl. IX, fig. 14) have by this stage undergone a further development. The mesoblastic somites are more fully developed. The general relations of these somites is shown in longitudinal section in Pl. IX, fig. 15, and in transverse section in Pl. IX, fig. 14. In the tail, where they are simplest (shown on the upper side in fig. 14), each mesoblastic somite is formed of a somatic layer of more or less cubical cells attached to the epiblast, and a splanchnic layer of flattened cells. Between the two is placed a completely circumscribed cavity, which constitutes part of the embryonic body cavity. Between the yolk and the splanchnic layer are placed a few scattered cells, which form the latest derivatives of the yolk-cells, and are to be reckoned as part of the splanchnic mesoblast. The mesoblastic somites do not extend outwards beyond the edge of the ventral plate, and the corresponding mesoblastic somites of the two sides do not nearly meet in the middle line. In the limb-bearing somites the mesoblast has the same general characters as in the posterior somites, but the *somatic* layer is prolonged as a hollow papilliform process into the limb, so that each limb has an axial cavity continuous with the section of the body cavity of its somite. The description given by Metschnikoff of the formation of the mesoblastic somites in the scorpion, and their continuation into the limbs, closely corresponds with the history of these parts in spiders. In the region of each procephalic lobe the mesoblast is present as a continuous layer underneath the epiblast, but in the earlier part of the stage, at any rate, is not formed of two distinct layers with a cavity between them.

The epiblast at this stage has also undergone important changes. Along the median ventral groove it has become very thin. On each side of this groove it exhibits in each appendage-bearing somite a well-marked thickening, which gives in surface views the appearance of a slightly raised area (Pl. VIII, fig. 5), between each appendage and the median line. These thickenings are the first rudiments of the ventral nerve ganglia. The ventral nerve cord at this stage is thus formed of two ridge-like thickenings of the epiblast, widely separated in the median line, each of which is constituted of a series of raised divisions—the ganglia (fig. 14, *vg*)—united by shorter, less prominent divisions. The nerve cords are formed from before backwards, and are not at this stage found in the hinder segments. *There is a distinct* *ganglionic thickening for the cheliceræ quite independent of the procephalic lobes.*

In the procephalic lobes the epiblast is much thickened, and is formed of several rows of cells. The greater part of it is destined to give rise to the supra-œsophageal ganglia.

During the various changes which have been described the blastoderm cells have been continually dividing, and, together with their nuclei, have become considerably smaller than at first. The yolk cells have in the meantime remained much as before, and are, therefore, considerably larger than the nuclei of the blastoderm cells. They are more numerous than in the earlier stages, but are still surrounded by a protoplasmic body, which is continued into a protoplasmic reticulum. The yolk is still divided up into polygonal segments, but from sections it would appear that the nuclei are more numerous than the segments, though I have failed to arrive at quite definite conclusions on this point.

As development proceeds the appendages grow longer and gradually bend inwards. They become very soon divided by a series of ring-like constrictions which constitute the first indications of the future joints (Pl. VII, fig. 6). The full number of joints are not at once reached, but in the ambulatory appendages five only appear at first to be formed. There are four joints in the pedipalpi, while the cheliceræ do not exhibit any signs of becoming jointed till somewhat later. The primitive presence of only five joints in the ambulatory appendages is interesting, as this number is permanent in Insects and in Peripatus.

The next stage figured forms the last of the third period (Pl. VIII, fig. 7 and 7 *a*). The ventral plate is still rolled round the egg (fig. 7), and the end of the tail and the procephalic lobes nearly meet dorsally, so that there is but a very slight development of the dorsal region. There are the same number of segments as before, and the chief differences in appearance between the present and the previous stage depend upon the fact (1) that the median ventral integument between the nerve ganglia has become wider, and at the same time thinner; (2) that the limbs have become much more developed; (3) that the stomodæum is definitely established; (4) that the procephalic lobes have undergone considerable development.

Of these features, the three last require a fuller description. The limbs of the two sides are directed towards each other, and nearly meet in the ventral line. The cheliceræ are two-jointed, and terminate in what appear like rudimentary chelæ, a fact which perhaps indicates that the spiders are descended from ancestors with chelate cheliceræ. The four embryonic post-ambulatory appendages are now at the height of their development.

The stomodæum (Pl. VIII, fig. 7, and Pl. IX, fig. 17, *st*) is a deepish pit between the two procephalic lobes, and distinctly in front of segment of the cheliceræ. It is bordered in front by a large, well-marked, bilobed upper lip, and behind by a smaller lower lip. The large upper lip is a temporary structure, to be compared, perhaps, with the gigantic upper lip of the embryo of Chelifer (cf. Metschinkoff). On each side of and behind the mouth two whitish masses are visible, which are the epiblastic thickenings which constitute the ganglia of the cheliceræ (Pl. VIII, fig. 7, *ch. g*).

The procephalic lobes (*pr. l*) now form two distinct masses, and each of them is marked by a semicircular groove, dividing it into a narrower anterior and a broader posterior division.

In the region of the trunk the general arrangement of the germinal layers has not altered to any great extent. The ventral ganglionic thickenings are now developed in all the segments in the abdominal as well as in the thoracic region. The individual thickenings themselves, though much more conspicuous than in the previous stage (Pl. IX, fig. 16, *v. c*), are still integral parts of the epiblast. They are more widely separated than before in the middle line. The mesoblastic somites retain their earlier constitution (Pl. IX, fig. 16). Beneath the procephalic lobes the mesoblast has, in most respects, a constitution similar to that of a mesoblastic somite in the trunk. It is formed of two bodies, one on each side, each composed of a splanchnic and somatic layer (Pl. IX, fig. 17, *sp.* and *so*), enclosing between them a section of the body-cavity. But the cephalic somites, unlike those of the trunk, are united by a median bridge of mesoblast, in which no division into two layers can be detected. This bridge assists in forming a thick investment of mesoblast round the stomodæum (*st*).

The existence of a section of the body cavity in the præoral region is a fact of some interest, especially when taken in connection with the discovery, by Kleinenberg, of a similar structure in the head of Lumbricus. The procephalic lobe represents the præoral lobe of Chætopod larvæ, but the prolongation of the body cavity into it does not, in my opinion, necessarily imply that it is equivalent to a post-oral segment.

The epiblast of the procephalic lobes is a thick layer several cells deep, but without any trace of a separation of the ganglionic portion from the epidermis.

The nuclei of the yolk have increased in number, but the yolk, in other respects, retains its earlier characters.

The next period in the development is that in which the body of the embryo gradually acquires the adult form. The most important event which takes place during this period is the development of the dorsal region of the embryo, which, up to its commencement, is practically non-existent. As a consequence of the development of the dorsal region, the embryo, which has hitherto had what may be called a dorsal flexure, gradually unrolls itself, and acquires a ventral flexure. This change in the flexure of the embryo is in appearance a rather complicated phenomenon, and has been somewhat differently described by the two naturalists who have studied it in recent times.

For Claparède the prime cause of the change of flexure is the translation dorsalwards of the limbs. He compares the dorsal region of the embryo to the arc of a circle, the two ends of which are united by a cord formed by the line of insertion of the limbs. He points out that if you bring the middle of the cord, so stretched between the two ends of the arc, nearer to the summit of the arc, you necessarily cause the two ends of the arch to approach each other, or, in other words, if the insertion of the limbs is drawn up dorsally, the head and tail must approach each other ventrally.

Barrois takes quite a different view to that of Claparède, which will perhaps be best understood if I quote a translation of his own words. He says: "At the period of the last stage of the embryonic band (the stage represented in Pl. IX, fig. 7, in the present paper) this latter completely encircles the egg, and its posterior extremity nearly approaches the cephalic region. Finally, the germinal bands, where they unite at the anal lobe (placed above on the dorsal surface), form between them a very acute angle. During the following stages one observes the anal segment separate further and further from the cephalic region, and approach nearer and nearer to the ventral region. This displacement of the anal segment determines, in its turn, a modification in the divergence of the anal bands; the angle which they form at their junction tends to become more obtuse. The same processes continue regularly till the anal segment comes to occupy the opposite extremity to the cephalic region, a period at which the two germinal bands are placed in the same plane and the two sides of the obtuse angle end by meeting in a straight line. If we suppose a continuation of the same phenomenon it is clear that the anal segment will come to occupy a position on the ventral surface, and the germinal bands to approach, but in the inverse way, so as to form an angle opposite to that which they formed at first. This condition ends the process by which the posterior extremity of the embryonic band, at first directed towards the dorsal side, comes to bend in towards the ventral region."

Neither of the above explanations is to my mind perfectly satisfactory. The whole phenomenon appears to me to be very simple, and to be caused by the elongation of the dorsal region, *i.e.* the region on the dorsal surface between the anal and procephalic lobes. Such an elongation necessarily separates the anal and procephalic lobes; but, since the ventral plate does not become shortened in the process, and the embryo cannot straighten itself on account of the egg-shell, it necessarily becomes flexed, and such flexure can only be what I have already called a ventral flexure. If there were but little food yolk this flexure would cause the whole embryo to be bent in, so as to have the ventral surface concave, but instead of this the flexure is confined at first to the two bands which form the ventral plate. These bands are bent in the natural way (Pl. VIII, fig. 8, B), but the yolk forms a projection,a kind of yolk sack as Barrois calls it, distending the thin integument between the two ventral bands. This yolk sack is shown in surface view in Pl. VIII, fig. 8, and in section in Pl. X, fig. 18. At a later period, when the yolk has become largely absorbed in the formation of various organs, the true nature of the ventral flexure becomes apparent, and the abdomen of the young Spider is found to be bent over so as to press against the ventral surface of the thorax (Pl. VIII, fig. 9). This flexure is shown in section in Pl. X, fig. 21.

At the earliest stage of this period of which I have examples, the dorsal region has somewhat increased, though not very much. The limbs have grown very considerably and *now cross in the middle line.*

The ventral ganglia, though not the supra-œsophageal, have become separated from the epiblast.

The yolk nuclei, each surrounded by protoplasm as before, are much more numerous.

In other respects there are no great changes in the internal features.

In my next stage, represented in Pl. VIII, figs. 8 *a*, and 8 *b*, a very considerable advance has become effected. In the first place the dorsal surface has increased in length to rather more than one half the circumference of the ovum.

The dorsal region has, however, not only increased in length, but also in definiteness, and a series of transverse markings (fig. 8 *a* and *b*), which are very conspicuous in the case of the four anterior abdominal segments (the segments with rudimentary appendages), have appeared, indicating the limits of segments dorsally. The terga of the somites may, in fact, be said to have become formed. The posterior terga (fig. 8 *a*) are very narrow compared to the anterior.

The caudal protuberance is more prominent than it was, and somewhat bilobed; it is continued on each side into one of the bands, into which the ventral plate is divided. These bands, as is best seen in side view (fig. 8 *b*), have a ventral curvature, or, perhaps more correctly, are formed of two parts, which meet at a large angle open towards the ventral surface. The posterior of these parts bears the four still very conspicuous provisional appendages, and the anterior the six pairs of thoracic appendages. The four ambulatory appendages are now seven-jointed, as in the adult, but though longer than in the previous stage they do not any longer *cross or even meet in the middle line*, but are, on the contrary, separated by a very considerable interval. This is due to the great distension by the yolk of the ventral part of the body, in the interval between the two parts of the original ventral plate. The amount of this yolk may be gathered from the section (Pl. X, fig. 18). The pedipalpi carry a blade on their basal joint. The cheliceræ no longer appear to spring from an independent post-oral segment.

There is a conspicuous lower lip, but the upper lip is less prominent than before. Sections at this stage show that the internal changes have been nearly as considerable as the external.

The dorsal region is now formed of a (1) flattened layer of epiblast cells, and a (2) fairly thick layer of large and rather characteristic cells which any one who has studied sections of spider's embryos will recognise as derivatives of the yolk. These cells are not, therefore, derived from prolongations of the somatic and splanchnic layers of the already formed somites, but are new formations derived from the yolk. They commenced to be formed at a much earlier period, and some of them are shown in the long section (Pl. IX, fig. 15). In the next stage these cells become differentiated into the somatic and splanchnic mesoblast layers of the dorsal region of the embryo.

In the dorsal region of the abdomen the heart has already become established. So far as I have been able to make out it is formed from a solid cord of the cells of the dorsal region. The peripheral layer of this cord gives rise to the walls of the heart, while the central cells become converted into the corpuscles of the blood.

The rudiment of the heart is in contact with the epiblast above, and there is no greater evidence of its being derived from the splanchnic than from the somatic mesoblast; it is, in fact, formed before the dorsal mesoblast has become differentiated into two layers.

In the abdomen three or four transverse septa, derived from the splanchnic mesoblast, grow a short way into the yolk. They become more conspicuous during the succeeding stage, and are spoken of in detail in the description of that stage. In the anterior part of the thorax a longitudinal and vertical septum is formed, which grows downwards from the median dorsal line, and divides the yolk in this region into two parts. In this septum there is formed at a later stage a vertical muscle attached to the suctorial part of the stomodæum.

The mesoblastic somites of the earlier stage are but little modified; and there are still prolongations of the body cavity into the limbs (Pl. X, fig. 18).

The lateral parts of the ventral nerve cords are now at their maximum of separation (Pl. X, fig. 18, *v. g*). Considerable differentiation has already set in in the constitution of the ganglia themselves, which are composed of an outer mass of ganglion cells enclosing a kernel of nerve fibres, which lie on the inner side and connect the successive ganglia. There are still distinct thoracic and abdominal ganglia for each segment, and there is also a pair of separate ganglion for the cheliceræ, which assists, however, in forming the œsophageal commissures.

The thickenings of the præoral lobe which form the supra-œsophageal ganglia are nearly though not quite separated from the epiblast. The semicircular grooves of the earlier stages are now deeper than before, and are well shown in sections nearly parallel to the outer anterior surface of the ganglion (Pl. X, fig. 19). The supra-œsophageal ganglia are still entirely formed of undifferentiated cells, and are without commissural tissue like that present in the ventral ganglia.

The stomodæum has considerably increased in length, and the proctodæum has become formed as a short, posteriorly directed involution of the epiblast. I have seen traces of what I believe to be two outgrowths from it, which form the Malpighian bodies.

The next stage constitutes (Pl. VIII, fig. 9) the last which requires to be dealt with so far as the external features are concerned. The yolk has now mainly passed into the abdomen, and the constriction separating the thorax and abdomen has began to appear. The yolk sack has become absorbed, so that the two halves of the ventral plate in the thorax are no longer widely divaricated. The limbs have to a large extent acquired their permanent structure, and the rings of which they are formed in the earlier stages are now replaced by definite joints. A delicate cuticle has become formed, which is not figured in my sections. The four rudimentary appendages have disappeared, unless, which seems to me in the highest degree improbable, two of them remain as the spinning mammillæ, which are now present. Behind is the anal lobe, which is much smaller and less conspicuous than in the previous stage. The spinnerets and anal lobe are shown as five papillæ in Pl. VIII, fig. 9. Dorsally the heart is now very conspicuous, and in front of the cheliceræ may be seen the supra-œsophageal ganglia.

The indifferent mesoblast has now to a great extent become converted into the permanent tissues. On the dorsal surface there was present in the last stage a great mass of unformed mesoblast cells. This mass of cells has now become divided into a somatic and splanchnic layer (Pl. X, fig. 22). It has, moreover, in the abdominal region at any rate, become divided up into somites. At the junction between the successive somites the splanchnic mesoblast on each side of the abdomen dips down into the yolk and forms a septum (Pl. X, fig. 22 *s*). The septa so formed, which were first described by Barrois, are not complete. The septa of the two sides do not, in the first place, quite meet along the median dorsal or ventral lines, and in the second place they only penetrate the yolk for a certain distance. Internally they usually end in a thickened border.

Along the line of insertion of each of these septa there is developed a considerable space between the somatic and splanchnic layers of mesoblast. The parts of the body cavity so established are transversely directed channels passing from the heart outwards. They probably constitute the venous spaces, and perhaps also contain the transverse aortic branches.

In the intervals between these venous spaces the somatic and splanchnic layers of mesoblast are in contact with each other.

I have not been able to work out satisfactorily the later stages of development of the septa, but I have found that they play an important part in the subsequent developmen of the abdomen. In the first place they send off lateral offshoots, which unite the various septa together, and divide up the cavity of the abdomen into a number of partially separated compartments. There appears, however, to be left a free axial space for the alimentary tract, the mesoblastic walls of which are, I believe, formed from the septa.

At the present stage the splanchnic mesoblast, apart from the septa, is a delicate membrane of flattened cells (fig. 22, *sp*). The somatic mesoblast is thicker, and is formed of scattered cells (*so*).

The somatic layer is in part converted, in the posterior region of the abdomen, into a delicate layer of longitudinal muscles, the fibres of which are not continuous for the whole length of the body, but are interrupted at the lines of junction of the successive segments. They are not present in the anterior part of the abdomen. The longitudinal direction of these fibres, and their division with myotomes, is interesting, since both these characters, which are preserved in Scorpions, are lost in the abdomen of the adult Spider.

The original mesoblastic somites have undergone quite as important changes as the dorsal mesoblast. In the abdominal region the somatic layer constitutes two powerful bands of longitudinal muscles, inserted anteriorly at the root of the fourth ambulatory appendage, and posteriorly at the spinning mammillæ. Between these two bands are placed the nervous bands. The relation of these parts are shown in the section in Pl. X, fig. 20 *d*, which cuts the abdomen horizontally and longitudinally. The mesoblastic bands are seen at *m.*, and the nervous bands within them at *ab. g.* In the thoracic region the part of the somatic layer in each limb is converted into muscles, which are continued into dorsal and ventral muscles in the thorax (*vide* fig. 20 *c*). There are, in addition to these, intrinsic transverse fibres on the ventral side of the thorax. Besides these muscles there are in the thorax, attached to the suctorial extremity of the stomodæum, three powerful muscles, which I believe to be derived from the somatic mesoblast. One of these passes vertically down from the dorsal surface, in the septum the commencement of which was described in the last stage. The two other muscles are lateral, one on each side (Pl. IX, fig. 20 *c*).

The heart has now, in most respects, reached its full development. It is formed of an outer muscular layer, within which is a doubly-contoured lining, containing nuclei at intervals, which is probably of the nature of an epithelioid lining (Pl. X, fig. 22 *ht*). In its lumen are numerous blood-corpuscles (not represented in my figure). The heart lies in a space bound below by the splanchnic mesoblast, and to the sides by the somatic mesoblast. This space forms a kind of pericardium (fig. 22 *pc*), but dorsally the heart is in contact with the epiblast. The arterial trunks connected with it are fully established.

The nervous system has undergone very important changes.

In the abdominal region the ganglia of each side have fused together into a continuous cord (fig. 21 *ab. g.*). In fig. 20, in which the abdomen is cut horizontally and longitudinally, there are seen the two abdominal cords (*ab. g.*) united by two transverse commissures; and I believe that there are at this stage three or four transverse commissures at any rate, which remain as indications of the separate ganglia, from the coalescence of which the abdominal cords are formed. The two abdominal cords are parallel and in close contact.

In the thoracic region changes of not less importance have taken place. The ganglia are still distinct. The two cords formed of these ganglia are no longer widely separated, but meet, in the usual way, in the ventral line. Transverse commissures have become established (fig. 20 *c, pd. g.*), between the ganglia of the two sides. There is as little trace at this, as at the previous stages, of an ingrowth of epiblast, to form a median portion of the central nervous system. Such a median structure has been described by Hatschek for Lepidoptera, and he states that it gives rise to the transverse commissures between the ganglia. My observations show that for the spider, at any rate, nothing of the kind is present.

As shown in the longitudinal section (Pl. X, fig. 21), the ganglion of the cheliceræ has now united with the supra-œsophageal ganglion. It forms, as is shown in fig. 20 *b* (*ch. g.*), a part of the œsophageal commissure, and there is no sub-œsophageal commissure uniting the ganglia of the cheliceræ, but the œsophageal ring is completed below by the ganglia of the pedipalpi (fig. 20 *c, pd. g.*).

The supra-œsophageal ganglia have become completely separated from the epiblast.

I have unfortunately not studied their constitution in the adult, so that I cannot satisfactorily identify the parts which can be made out at this stage.

I distinguish, however, the following regions:

(1) A central region containing the commissural part, and continuous below with the ganglia of the cheliceræ.

(2) A dorsal region formed of two hemispherical lobes.

(3) A ventral anterior region.

The central region contains in its interior the commissural portion, forming a punctiform rounded mass in each ganglion: a transverse commissure connects the two masses (*vide* fig. 20 *b*).

The dorsal hemispherical lobes are derived from the part which, at the earlier stage, contained the semicircular grooves. When the supra-œsophageal ganglia become separated from the epidermis the cells lining these grooves become constricted off with them, and form part of these ganglia. Two cavities are thus formed in this part of the supra-œsophageal ganglia. These cavities become, for the most part, obliterated, but persist at the outer side of the hemispherical lobes (figs. 20 *a* and 21).

The ventral lobe of the brain is a large mass shown in long section in fig. 21. It lies immediately in front of and almost in contact with the ganglia of the cheliceræ.

The two hemispherical lobes agree in position with the fungiform body (pilzhutförmige Korpern), which has attracted so much the attention of anatomists, in the supra-œsophageal ganglia of Insects and Crustacea; but till the adult brain of Spiders has been more fully studied it is not possible to state whether the hemispherical lobes become the fungiform bodies.

Hatschek[1] has described a special epiblastic invagination in the supra-œsophageal ganglion of Bombyx, which is probably identical with the semicircular groove of Spiders and Scorpions, but in the figure he gives the groove does not resemble that in the Arachnida. A similar groove is found in Peripatus, and there forms, as I have found, a large part of the supra-œsophageal ganglia. It is figured by Moseley, 'Phil. Trans.,' vol. 164, pl. lxxv, fig. 9.

The stomodæum is considerably larger than in the last stage, and is lined by a cuticle; it is a blind tube, the blind end of which is the suctorial pouch of the adult. To this pouch are attached the vertical dorsal, and two lateral muscles spoken of above.

The proctodæum (*pr.*) has also grown in length, and the two Malpighian vessels which grow out from its blind extremity (fig. 20 *e*, *mp. g.*) have become quite distinct. The part now formed is the rectum of the adult. The proctodæum is surrounded by a great mass of splanchnic mesoblast. The mesenteron has as yet hardly commenced to be developed. There is, however, a short tube close to the proctodæum (fig. 20 *e*, *mes*), which would seem to be the commencement of it. It

---

[1] "Beiträge z. Entwick d. Lepidopteren," 'Jenaische Zeit.,' vol. xi, p. 124.

ends blindly on the side adjoining the rectum, but is open anteriorly towards the yolk, and there can be very little doubt that it owes its origin to cells derived from the yolk. On its outer surface is a layer of mesoblast.

From the condition of the mesenteron at this stage there can be but little doubt that it will be formed, not on the surface, *but in the interior of the yolk.* I failed to find any trace of an anterior part of the mesenteron adjoining the stomodæum. In the posterior part of the thorax (*vide* fig. 20 *d*), there is undoubtedly no trace of the alimentary tract.

The presence of this rudiment shows that Barrois is mistaken in supposing that the alimentary canal is formed entirely from the stomodæum and proctodæum, which are stated by him to grow towards each other, and to meet at the junction of the thorax and abdomen. My own impression is that the stomodæum and proctodæum have reached their full extension at the present stage, and that both the stomach in the thorax and the intestine in the abdomen are products of the mesenteron.

The yolk retains its earlier constitution, being divided into polygonal segments, formed of large yolk vesicles. The nuclei are more numerous than before. In the thorax the yolk is anteriorly divided into two lobes by the vertical septum, which contains the vertical muscle of the suctorial pouch. In the posterior part of the thorax it is undivided.

I have not yet been able clearly to make out the eventual fate of the yolk. At a subsequent stage, when the cavity of the abdomen is cut up into a series of compartments by the growth of the septa, described above, the yolk fills these compartments, and there is undoubtedly a proliferation of yolk cells round the walls of these compartments. It would not be unreasonable to conclude from this that the compartments were destined to form the hepatic cæca, each cæcum being enclosed in a layer of splanchnic mesoblast, and its hypoblastic wall being derived from the yolk cells. I think that this hypothesis is probably correct, but I have met with some facts which made me think it possible that the thickenings at the ends of the septa, visible in Pl. X, fig. 22, were the commencing hepatic cæca.

I must, in fact, admit that I have hitherto failed to work out satisfactorily the history of the mesenteron and its appendages. The firm cuticle of young spiders is an obstacle both in the way of making sections and of staining, which I have not yet overcome.

General Conclusions.

Without attempting to compare at length the development of the spiders with that of other Arthropoda, I propose to point out a few features in the development of spiders, which appear to show that the Arachnida are undoubtedly more closely related to the other Tracheata than to the Crustacea.

The whole history of the formation of the mesoblast is very similar to that in insects. The mesoblast in both groups is formed by a thickening of the median line of the ventral plate (germinal streak).

In insects there is usually formed a median groove, the walls of which become converted into a plate of mesoblast. In spiders there is no such groove, but a median keel-like thickening of the ventral plate (Pl. IX, fig. 11), is very probably an homologous structure. The unpaired plate of mesoblast formed in both insects and Arachnida is exactly similar, and beomes divided, in both groups, into two bands, one on each side of the middle line. Such differences as there are between Insects and Arachnida sink into insignificance compared with the immense differences in the origin of the mesoblast between either group, and that in the Isopoda, or, still more, the Malacostraca and most Crustacea. In most Crustacea we find that the mesoblast is budded off from the walls of an invagination, which gives rise to the mesenteron.

In both spiders and Myriopoda, and probably insects, the mesoblast is subsequently divided into somites, the lumen of which is continued into the limbs. In Crustacea mesoblastic somites have not usually been found, though they appear occasionally to occur, *e.g.* Mysis, but they are in no case similar to those in the Tracheata.

In the formation of the alimentary tract, again, the differences between the Crustacea and Tracheata are equally marked, and the Arachnida agree with the Tracheata. There is generally in Crustacea an invagination, which gives rise to the mesenteron. In Tracheata this never occurs. The proctodæum is usually formed in Crustacea before or, at any rate, not later than the stomodæum.[1] The reverse is true for the Tracheata. In Crustacea the proctodæum and stomodæum, especially the former, are very long, and usually give rise to the greater part of the alimentary tract, while the mesenteron is usually short.

---

[1] If Grobben's account of the development of Moina is correct this statement must be considered not to be universally true.

In the Tracheata the mesenteron is always considerable, and the proctodæum is always short. The derivation of the Malpighian bodies from the proctodæum is common to most Tracheata. Such organs are not found in the Crustacea.

With reference to other points in my investigations, the evidence which I have got that the chelicerae are true post-oral appendages supplied in the embryo from a distinct postoral ganglion, confirms the conclusions of most previous investigators, and shows that these appendages are equivalent to the mandibles, or possibly the first pair of maxilla of other Tracheata. The invagination, which I have found, of part of a groove of epiblast in the formation of the supra-œsophageal ganglia is of interest, owing to the wide extension of a similar occurrence amongst the Tracheata.

The wide divarication of the ventral nerve cords in the embryo renders it easy to prove that there is no median invagination of epiblast between them, and supports Kleinenberg's observations on Lumbricus as to the absence of this invagination. I have further satisfied myself as to the absence of such an invagination in Peripatus. It is probable that Hatschek and other observers who have followed him are mistaken in affirming the existence of such an invagination in either the Chætopoda or the Arthropoda.

The observations recorded in this paper on the yolk cells and their derivations are, on the whole, in close harmony with the observations of Dohrn, Bobretsky, and Graber, on Insects. They show, however, that the first formed mesoblastic plate does not give rise to the whole of the mesoblast, but that during the whole of embryonic life the mesoblast continues to receive accessions of cells derived from the cells of the yolk.

Araneina.

1. *Balbiani*, "Mémoire sur le Développement des Araneides," 'Ann. Sci. Nat.,' series v, vol. xvii, 1873.
2. *J. Barrois*, "Recherches s. l. Développement des Araignées," 'Journal de l. Anat. e. de la Physiol.,' 1878.
3. *E. Claparède*, 'Recherches s. l'Evolution des Araignées,' Utrecht, 1860.
4. *Herold*, 'De Génératione Araniorum in Ovo,' Marburg, 1824.
5. *H. Ludwig*, "Ueb. d. Bildung des Blastoderm," bie d. Spinnen, 'Zeit. f. wiss. Zool.,' vol. xxvi, 1876.

Postscript to the Paper on the Development of the Araneina

Since the publication of the preceding paper, my attention has been called to a very important paper by Salensky, on the "Development of the Araneina," written in Russian, which appeared in 1871 in the 'Kiew Society of Naturalists.' An abstract of this paper is published in Hofmann and Schwalbe's 'Jahresberichte' for 1878. From the abstract it appears that Salensky was able to carry his investigations a good deal further than previous investigators. He detected the nuclei in the yolk, and showed that they gave rise in part to the inner layer of blastoderm cells. He further showed that the mesoblast became split into splanchnic and somatic layers, and gave an account of the development of the heart, similar to that in my paper. He believes that the third and fourth pairs of provisional abdominal appendages become the spinning mammillæ; while the anterior pair gives rise to the pulmonary sacs. I was myself unable to follow in detail the disappearance of the four provisional appendages, though from various considerations I was led to reject the view that the third and fourth pairs became the spinning mammillæ. I could not moreover trace the development of the pulmonary sacs from the first pair of abdominal appendages. Further observation on these points with fresh material are much required; and I hope myself, to be able before long, to return to this part of the development as well as to the history of the later stages.

On the DEVELOPMENT *of the* STRUCTURE KNOWN *as the* 'GLOMERULUS *of the* HEAD-KIDNEY' *in the* CHICK.

By ADAM SEDGWICK, B.A.

IN a paper by Mr. Balfour and myself (*vide* p. 1—20 of "these Studies"), describing the development of what we believed to be a rudimentary head-kidney in the chick, we drew attention to a structure which so closely resembled the glomerulus of the head-kidney of the Icthyopsida that we identified it as an homologous structure.

Gasser [1] has also independently discovered and similarly identified this structure.

In the paper just referred to no attempt was made to trace the development of this glomerulus, but it was merely described as it appeared at its time of greatest development.

The following description is taken from that paper:

"In the chick the glomerulus is paired and consists of a vascular outgrowth or ridge projecting into the body cavity on each side at the root of the mesentery. It extends from the anterior end of the Wolffian body to the point where the foremost opening of the head-kidney commences. We have found it at a period slightly earlier than that of the first development of the head-kidney. In the interior of this body is seen a stroma with numerous vascular channels and blood corpuscles, and a vascular connection is apparently becoming established, if it is not so already, between the glomerulus and the aorta. The stalk connecting the glomerulus with the attachment of the mesentery varies in thickness in different sections, but we believe that the glomerulus is continued unbroken throughout the very considerable region through which it extends. This point is, however, difficult to make sure of, owing to the facility with which the glomerulus breaks away. At the stage we are describing no true Malpighian bodies are present in the part of the Wolffian body on the same level with the anterior end of the glomerulus, but the Wolffian body merely consists of the Wolffian duct. At the level of the posterior part of the glomerulus this is no longer

---

[1] 'Sitzungsberichte der Gesellschaft zur Beförd d. gesam. Naturwiss.,' No. 5, 1879.

the case, but here a regular series of primary Malpighian bodies is present, and the glomerulus of the head-kidney may frequently be seen in the same section as a Malpighian body. In most sections the two bodies appear quite disconnected, but in those sections in which the glomerulus of the Malpighian body comes into view it is seen to be derived from the same formation as the glomerulus of the head-kidney."

The point which is left in doubt in the above description, viz. as to whether the glomerulus constitutes a continuous structure, is at once decided by a study of its development.

I may here state that it is not a continuous structure, but consists of a series of external glomeruli, each of which corresponds and is continuous with the glomeruli of the Malpighian bodies found in this part of the trunk.

I will commence the description of the development at the time when the segmental tubes have reached the stage of development figured by Kölliker[1] and myself.[2] At this stage each of them in the anterior region of the Wolffian body has the form of an **S**-shaped string, with a narrow opening into the body cavity, the lower limb of the **S** being formed by the intermediate cell mass, and the upper limb by a column of cells which connects the intermediate cell mass with the Wolffian duct.

In the region where each external glomerulus is afterwards found the openings into the body cavity, which are homologous with the peritoneal openings of the segmental tubes in Elasmobranchs, widen out very considerably, and a lumen is continued from them into the intermediate cell mass on the one hand, and on the other hand into the column of cells which forms the upper limb of the **S** and connects the intermediate cell mass with the Wolffian duct.[3]

That part of the segmental tube which will afterwards become a Malpighian body is therefore, in the region where an external glomerulus will subsequently be formed, connected with the body cavity by a short tube. This tube rapidly widens out, especially

---

[1] 'Entwicklungsgeschichte des Menschen u. der höheren Thiere,' p. 201, 2nd ed.

[2] 'Development of the Kidney, &c.,' p. 62 of "these Studies," Pl. VI, fig. 1.

[3] This may best be understood by examining fig. 11, Pl. VI, in my paper already referred to. If the primary Wolffian tubule (*wt*^{1}), here represented, were connected with the peritoneal epithelium at the point where the line from *wt*^{1} cuts it, and it were open to the body-cavity at that point, an appearance similar to that which I have attempted to describe would be obtained. Or perhaps a better idea of the structure may be obtained from fig. 6, Pl. XX, in Balfour's 'Monograph on the Development of Elasmobranch Fishes.' If *st* were very short and wide, so that *mg* were widely open to the body-cavity, the figure would resemble a developing Wolffian tubule in this anterior part of the chick's Wolffian body.

anteriorly, to such an extent that it soon appears as a shallow bay in the body cavity. Thus each opening at this stage forms a bay, wide and shallow anteriorly, becoming deeper and narrower as we pass backwards, until finally behind it is separated from the body cavity altogether, and there is seen in section a Malpighian capsule precisely resembling a developing Malpighian capsule in the hinder region of the Wolffian body.[1] This bay and in the small chamber behind, continuous with the bay but separated from the body cavity, are together serially homologous with a Malpighian capsule and the funnel leading from it into the body cavity. In them a small glomerulus soon appears attached to the dorsal wall. The glomerulus increases in size, and the bay anteriorly widens out very much, while behind it remains deep, and finally passes into the closed posterior portion. The glomerulus fills up this passage which clearly runs obliquely backwards and dorsalwards, and eventually, as far as I can ascertain, the opening becomes completely closed, the epithelium on the external glomerulus being no longer continued through the opening on to the internal glomerulus.

The external glomerulus, then, in the chick which has hitherto been known as the glomerulus of the head-kidney, is nothing more than a series of glomeruli of primary Malpighian bodies projecting through the wide openings of the segmental tubes into the body cavity. Their extreme antero-posterior extension may be said to be within the ninth and thirteenth segments.

In the chick the primary segmental tubes corresponding to these external glomeruli are apparently never fully developed.

I may mention that the external glomeruli are present in greater numbers and attain a greater development in the duck than in the chick.

I defer the details and all discussion of this extraordinary and unexpected development until I am able to publish a fuller paper with figures.

---

[1] Loc. cit., fig. 11.

DESCRIPTION OF PLATES I, II,

Illustrating paper "On the Existence of a Head-Kidney in the Embryo Chick, and on Certain Points in the Development of the Müllerian Duct."

COMPLETE LIST OF REFERENCE LETTERS.

ao. Aorta. *c. v.* Cardinal vein. *gl.* Glomerulus. gr_1. First groove of head-kidney. gr_2. Second groove of head-kidney. gr_3. Third groove of head-kidney. *g. e.* Germinal epithelium. *mr. b.* Malpighian body. *me.* Mesentery. *m. d.* Müllerian duct. r_1. First ridge of head-kidney. r_2. Second ridge of head-kidney. r_3. Third ridge of head-kidney. *W. d.* Wolffian duct. *x.* Fold in germinal epithelium.

EXPLANATION OF PLATE I.

SERIES A.—Sections through the head-kidney at our second stage. Zeiss, 2, ocul. 3 (reduced one third). The second and third grooves are represented with the ridge connecting them, and the rod of cells running backwards for a short distance.

No. 1.—Section through the second groove.

No. 2.—Section through the ridge connecting the second and third grooves.

No. 3.—Section passing through the same ridge at a point nearer the third groove.

Nos. 4, 5, 6.—Sections through the third groove.

No. 7.—Section through the point where the third groove passes into the solid rod of cells.

No. 8.—Section through the rod when quite separated from the germinal epithelium.

No. 9.—Section very near the termination of the rod.

No. 10.—Last section in which any trace of the rod is seen.

SERIES B.—Sections passing through the head-kidney at our third stage. Zeiss, C, ocul. 2. Our figures are representations of the following sections of the series, section 1 being the first which passes through the anterior groove of the head-kidney.

No. 1	SECTION 3.	No. 8	SECTION 13.
„ 2	„ 4.	„ 9	„ 15.
„ 3	„ 5.	„ 10	„ 16.
„ 4	„ 6.	„ 11	„ 17.
„ 5	„ 8.	„ 12	„ 18.
„ 6	„ 10.	„ 13	„ 19.
„ 7	„ 11.	„ 14	„ 20.

The Müllerian duct extends through eleven more sections.

The first groove (gr_1.) extends to No. 3.

The second groove (gr_2.) extends from No. 4 to No. 7.

The third groove (gr_3.) extends from No. 11 to No. 13.

The first ridge (r_1.) extends from No. 2 to No. 5.

The second ridge (r_2.) extends from No. 8 to No. 11.

The third ridge (r_3.) extends from No. 13 backwards through twelve sections, when it terminates by a pointed extremity.

FIG. C.—Section through the ridge connecting the second and third grooves of the head-kidney of an embryo slightly younger than that from which Series B. was taken. Zeiss, C, ocul. 3 (reduced one-third).

The fold of the germinal epithelium, which gives rise to a deep groove (*x.*) external to the head-kidney is well marked.

SERIES G.—Sections through the rod of cells constituting the termination of the Müllerian duct at a stage in which the head-kidney is still present. Zeiss, C, ocul. 2.

EXPLANATION OF PLATE II.

SERIES D.—Sections chosen at intervals from a complete series traversing the peritoneal opening of the Müllerian duct, the remnant of the head-kidney, and the termination of the Müllerian duct. Zeiss, C, ocul. 3 (reduced one-third).

Nos. 1 and 2.—Sections through the persistent anterior opening of the head-kidney (abdominal opening of Müllerian duct). The approach of the Wolffian duct to the groove may be seen by a comparison of these two figures. In the sections in front of these (not figured) the two are much more widely separated than in No. 1.

No. 3.—Section through the Müllerian duct, just posterior to the persistent opening.

Nos. 4 and 5.—Remains of the ridges, which at an earlier stage connected the first and second grooves, are seen passing from the Müllerian duct to the peritoneal epithelium.

No. 6.—Rudiment of the second groove (gr_2.) of the head-kidney.

Between 6 and 7 is a considerable interval.

No. 7.—All traces of this groove (gr_2.) have vanished, and the Müllerian duct is quite disconnected from the epithelium.

No. 8.—Rudiment of the third groove (gr_3.).

No. 9.—Müllerian duct quite free in the space between the peritoneal epithelium and the Wolffian duct, in which condition it extends until near its termination.

Between Nos. 9 and 10 is an interval of eight sections.

No. 10.—The penultimate section, in which the Müllerian duct is seen. A lumen cannot be clearly made out.

No. 11.—The last section in which any trace of the Müllerian duct is visible. No line of demarcation can be seen separating the solid end of the Müllerian duct from the ventral wall of the Wolffian duct.

FIGS. E. and F.—Sections through the glomerulus of the head-kidney from an embryo prior to the appearance of the head-kidney. Zeiss, B, ocul. 2. A comparison of the two figures shows the variation in the thickness of the stalk of the glomerulus. E.—Section anterior to the foremost Malpighian body. F.—Section through both the glomerulus of the head-kidney and that of a Malpighian body. The two are seen to be connected.

SERIES H.—Consecutive sections through the hind end of the Müllerian duct, from an embryo in which the head-kidney was only represented by a rudiment. (The embryo was, perhaps, very slightly older than that from which Series D was taken.) Zeiss, C, ocul. 3 (reduced one third).

No. 1.—Müllerian duct is without a lumen, and quite distinct from the Wolffian wall.

No. 2.—The solid end of the Müllerian duct is no longer distinct from the internal wall of the Wolffian duct.

No. 3.—All trace of the Müllerian duct has vanished.

SERIES I.—Sections through the hinder end of the Müllerian duct from an embryo of about the middle of the sixth day. Zeiss, C, ocul. 2 (reduced one third).

No. 1.—The Müllerian duct is distinct and small.

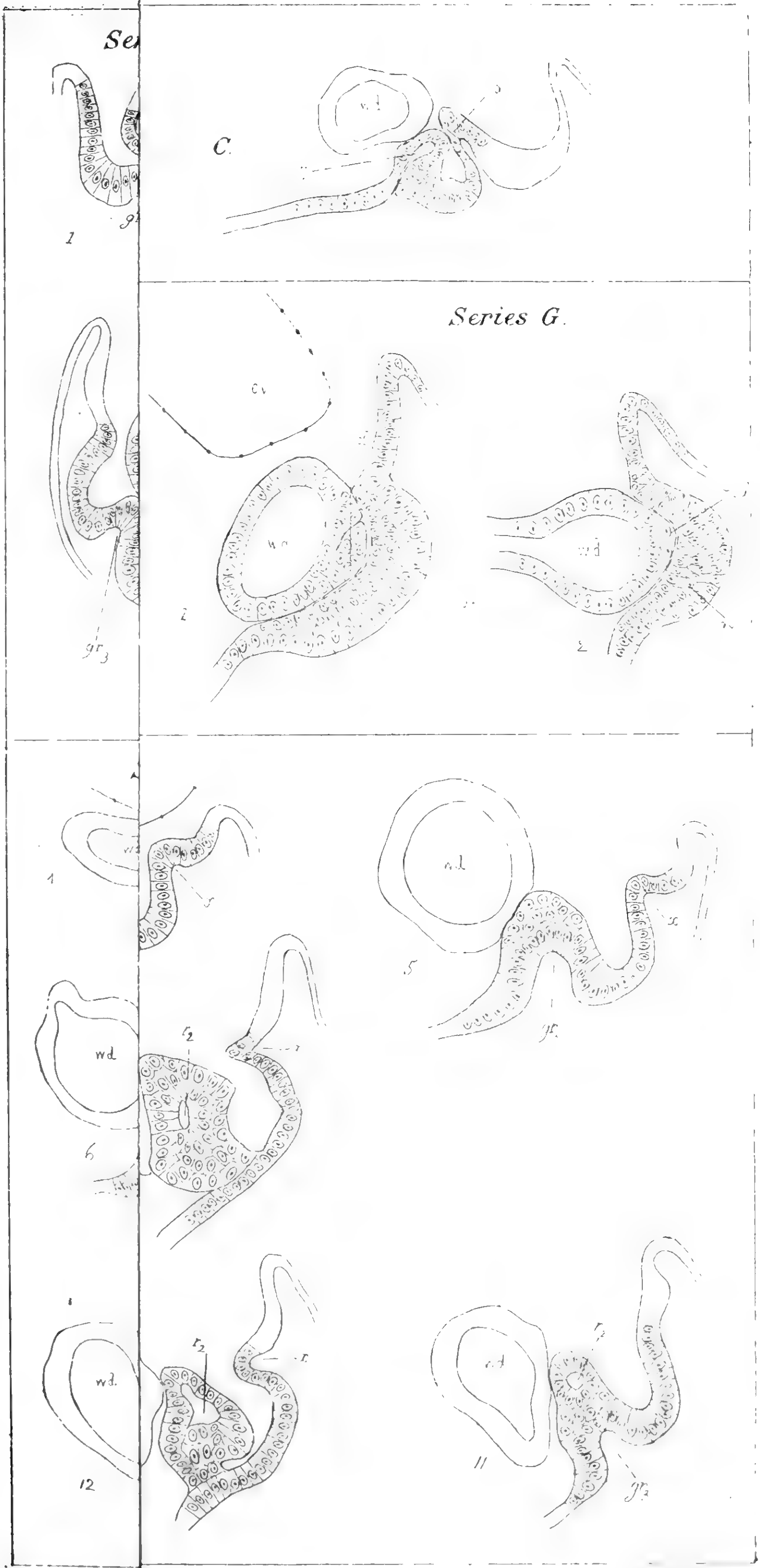
No. 2.—Is posterior by twelve sections to No. 1. The Müllerian duct is dilated, and its cells are vacuolated.

No. 3.—Penultimate section, in which the Müllerian duct is visible; it is separated by three sections from No. 2.

No. 4.—Last section in which any trace of the Müllerian duct is visible; the lumen, which was visible in the previous section, is now absent.

No. 5.—No trace of Müllerian duct. Nos. 3, 4, and 5, are consecutive sections.

FIG. K.—Section through the hind end of the abdominal opening of the Müllerian duct of a chick of 123 hours. Zeiss, C, ocul. 2 (reduced one-third). It illustrates the peculiar cord connecting the Müllerian and Wolffian ducts.



F.M. Balfour &

A.B. Balfour, sc.

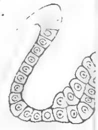
Series A

Series G

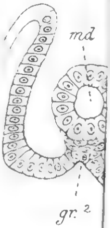
Series B

Series L

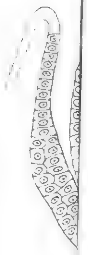
1.



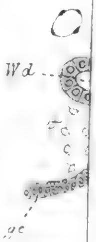
6.



11.



E.



F. M. Balfour

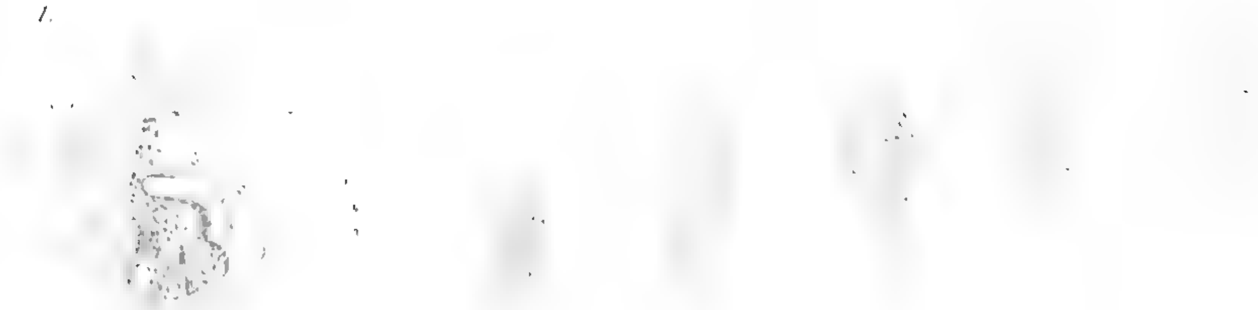


Plate III.

Series A

Fig 1

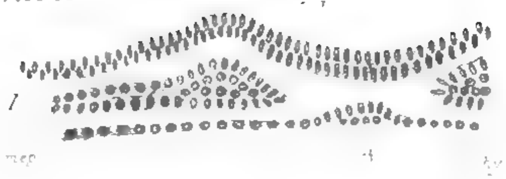


Fig 2

Fig 3

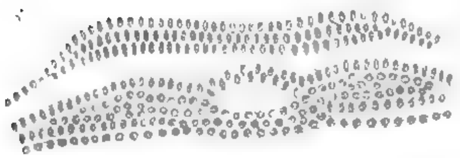


Fig 4

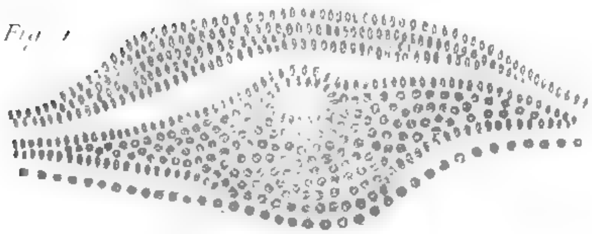
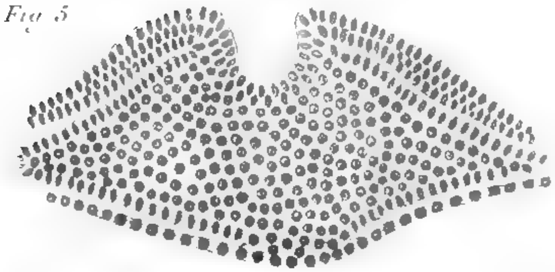


Fig 5



Series B

Fig 1

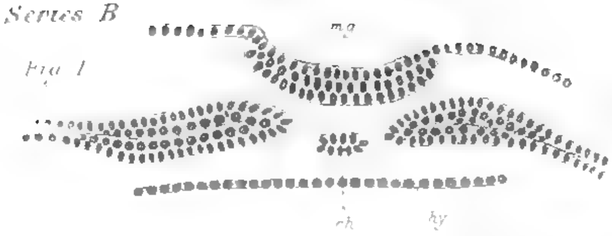


Fig 2

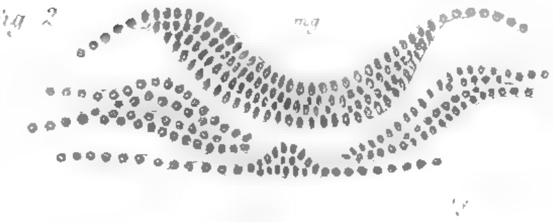


Fig 3

Fig 4

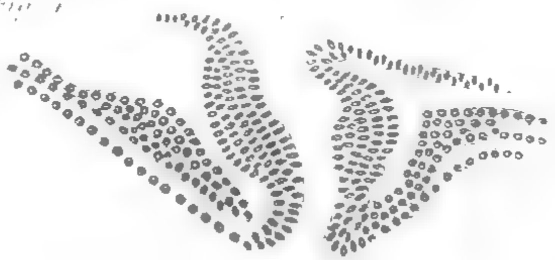


Fig 5

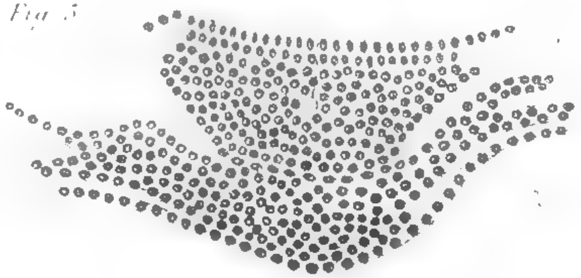


Fig B

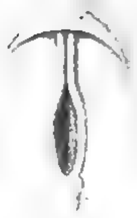


Fig C

F.M. Balfour, del'

F. Huth, lith' Edin'

DESCRIPTION OF PLATE III,

Illustrating paper on the "Early Development of the Lacertilia, together with some Observations on the Nature and Relation of the Primitive Streak."

Complete List of Reference Letters.

m. g. Medullary groove. *me. p.* Mesoplastic plate. *ep.* Epiblast. *hy.* Hypoblast. *ch'.* Notochordal thickening of hypoblast. *ch.* Notochord. *ne.* Neurenteric canal (blastopore). *pr.* Primitive streak. *am.* Amnion.

SERIES A.—Sections through an embryo shortly after the formation of the medullary groove. × 120.[1]

FIG. 1.—Section through the trunk of the embryo.

FIGS. 2—5.—Sections through the neurenteric canal.

FIG. B.—Surface view of a somewhat older embryo than that from which Series A is taken. × 30.

SERIES B.—Sections through the embryo represented in Fig. B. × 120.

FIG. 1.—Section through the trunk of the embryo.

FIGS. 2, 3.—Sections through the hind end of the medullary groove.

FIG. 4.—Section through the neurenteric canal.

FIG. 5.—Section through the primitive streak.

FIG. C.—Surface view of a somewhat older embryo than that represented in FIG. B. × 30.

---

[1] The spaces between the layers in these sections are due to the action of the hardening reagent.

EXPLANATION OF PLATES IV AND V,

Illustrating the Memoir on some Points in the Early Development of the Common Newt (*Triton tæniatus*), by W. B. Scott, B.A., and Henry F. Osborn, B.A.

With the exception of fig. 1 the following figures were drawn with a Zeiss' A objective. In figs. 2, 3, 4, 5, a No. 2 (Zeiss) eyepiece was used, and for figs. 6 and 7 a No. 3 eyepiece.

EXPLANATION OF PLATE IV.

List of References.

ep. Epiblast. *ep'.* Inner layer of epiblast. *yk.* Yolk. *hy.* Hypoblast. *in. hy.* Invagination hypoblast. *y. hy.* Yolk hypoblast. *m.* Mesoblast. *sp.* Splanchnopleure. *so.* Somatopleure. *al.* Alimentary canal. *nc.* Neural canal. *ch.* Notochord. *mg.* Medullary groove. *mf.* Medullary folds.

Fig. 1.—Longitudinal section of an embryo at time of commencement of invagination. Hartnack No. 7 obj., eyepiece 3. It shows one of the earliest stages of the epiblast.

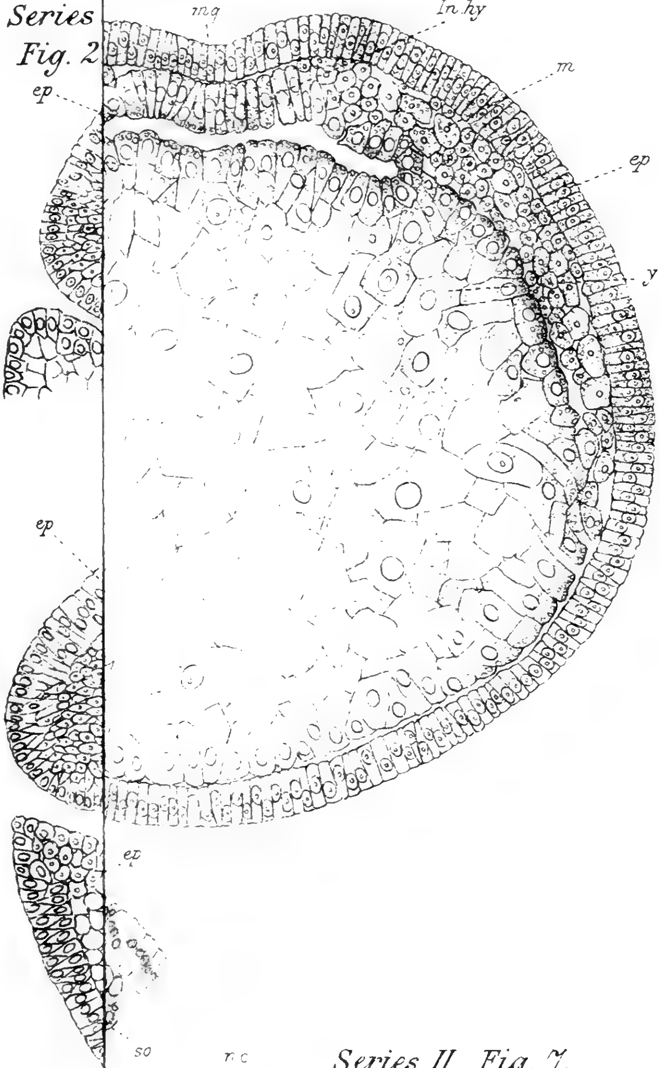
Fig. 2.—Represents a longitudinal section of a Triton embryo (probably *cristatus*) in the early part of Stage A. At the opening of the blastopore the section is in the median line. It slants off forwards, however, to one side, and therefore out of the region of the alimentary canal. It shows the formation of the invagination-hypoblast and the confused mass of cells arising from the reflection of the epiblast.

Fig. 3.—A section of the same embryo. It may be considered the reverse of the last. At the blastopore it is at one side of the median line, while anteriorly it is directly in the median line. This obliquity explains the apparent upgrowth of yolk-cells in the centre. Putting this and the previous section together, a fair idea may be obtained of the actual relation of the layers at this period. It illustrates the formation of mesoblast by invagination, and the obliteration of the segmentation cavity by the advance of the alimentary canal. The blastopore has been artificially widened.

Fig. 4.—An anterior transverse section of an embryo, at Stage A, slightly more advanced than the previous one. It shows the shallow medullary groove, the lateral plates of mesoblast extending half way down the sides, also the invagination-hypoblast above the alimentary canal continuous at the sides with the yolk hypoblast.

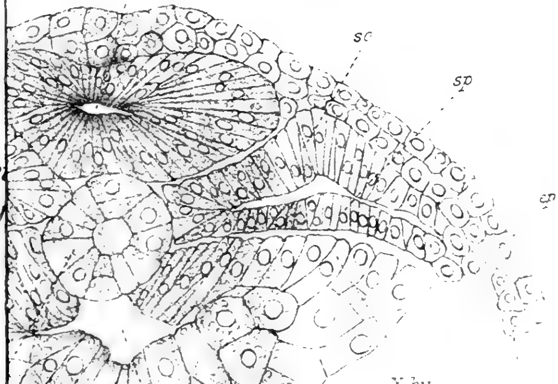
Fig. 5.—A transverse section through the head region of an embryo of

Series
Fig. 2



Series II, Fig. 7.

Ser
Fig



W B S. & H. F. O
F. Huth, Lith^{r} Edin^{r}

Series I Fig 1

[illegible]

[illegible]

Series I Fig 9

Series III Fig 10

Series III
Fig 15

F. Huth Lith^r Edin^r

EXPLANATION OF PLATE IV—*Continued.*

Stage B. It shows the splitting of the mesoblast and the formation of the medullary plate and notochord.

Fig. 6.—A transverse section through the trunk region of an embryo at Stage C, showing a slightly more advanced development than the last.

Fig. 7.—Represents a transverse section through the anterior trunk region late in Stage D.

EXPLANATION OF PLATE V.

List of References.

op. Optic vesicle. *pp.* Head cavities (numbered in order 1, 2, &c.) *vc.* Visceral clefts. *aa.* Aortic arches and auditory vesicles. *eb.* External branchia. *mb.* Mid brain. *hb.* Hind brain. *th.* Thyroid body. *al.* Alimentary canal. *ep.* Outer layer of epiblast. *ep'.* Inner layer of ditto. Zeiss. A, obj. oc. No. 2, except for figs. 9, 16, and 17.

Fig. 8.—Another transverse section in the middle region. This section is cut obliquely, so that the lateral and vertebral plates of mesoblast do not appear continuous with the mesoblast lining the sides of the embryo; it gives therefore at first sight a false impression.

Fig. 9.—Enlarged view of the lateral epiblast of fig. 6. Zeiss D, ocul. 3. *a.* One point of cell division.

Fig. 10.—Horizontal longitudinal section through the head of an embryo of Stage F. The section is slightly oblique, and hence unsymmetrical. It shows the unsegmented head cavity.

Fig. 11.—Vertical longitudinal section through the head of an embryo of Stage K, showing the relations of the head cavities, aortic arches, and gill clefts; it is taken too much at the side to show the thyroid.

Fig. 12.—Transverse section through head of an embryo of Stage I.

Fig. 13.—Transverse section of head of embryo very slightly older than the preceding figure.

Fig. 14.—Section through the same embryo as fig. 12, but considerably further forwards.

Fig. 15.—Transverse section through the head of an embryo of about Stage M.

Fig. 16.—External drawing of an embryo of Stage D. *s. r.* Sinus rhomboidalis.

Fig. 17.—External drawing of an embryo of Stage I. *o.* Oral involution.

EXPLANATION OF PLATES VI AND VII,

Illustrating Mr. Sedgwick's Memoir on "Development of the Kidney in its Relation to the Wolffian Body in the Chick."

Complete List of Reference Letters.

Ao. Aorta. *Al.* Alimentary canal. *cl.* Cloaca. *c. v.* Cardinal vein. *ep.* Epiblast. *hy.* Hypoblast. *i. c. m.* Intermediate cell mass. *i. c. m.'* Cell mass, which later becomes the intermediate cell mass. *m. e.* Mesentery. *M. d.* Müllerian duct. *k. b.* Kidney blastema. *k. t.* Kidney tubule. *n. c.* Notochord, *p.* Protovertebra. *p'.* Cell mass, which later becomes a protovertebra. *p. v.* Body-cavity. *p. e.* Peritoneal epithelium. *t.* Testis. *u.* Ureter. *ve.* Vertebral body. *w.* Wolffian body. *w. b.* Wolffian blastema. *w. d.* Wolffian duct. *w. t.*^{1} Primary Wolffian tubule. *w. t.*^{2} Secondary ditto. *w. t.*^{3} Tertiary ditto.

Fig. 1.—Section between the fifteenth and sixteenth protovertebræ of a chick with twenty-three protovertebræ, showing the rudimentary continuation of the body-cavity into the intermediate cell mass and the connection which the latter has obtained with the Wolffian duct. The intermediate cell mass in anterior and posterior neighbouring sections has separated from the peritoneal epithelium.

Figs. 2, 3, 4, and 5.—Sections taken from a duck embryo with about thirty-two protovertebræ, illustrating the development of the Wolffian tubules. Hart. cam., ob. 4.

Fig. 2.—Section through the thirtieth segment, intermediate cell mass continuous with peritoneal epithelium, and containing a rudimentary prolongation of the body-cavity. Lumen of Wolffian duct doubtful.

Fig. 3.—Section through the twenty-ninth segment, intermediate cell mass separate from peritoneal epithelium.

Fig. 4.—Section through the twenty-sixth protovertebra, showing features similar to above.

Fig. 5.—Section through the twenty-second protovertebra; commencing differentiation of Wolffian tubule.

Figs. 6—10.—Sections illustrating the more modified development of the Wolffian blastema, as seen in the chick behind the twentieth segment.

Fig. 6.—Section through a chick with twenty-six protovertebræ behind the last-formed segment, showing the thick peritoneal epithelium, the Wolffian blastema in connection with the mass of cells which will become a protovertebra. Hart. cam., ob. 4.

Fig. 7.—Section through the twenty-ninth protovertebra of a chick with twenty-nine protovertebræ, showing the thick peritoneal epithelium and the Wolffian blastema in connection with the protovertebræ. Hart. cam., ob. 4.

Fig. 8.—Section through the twenty-fourth segment of a chick with twenty-six protovertebræ, showing the Wolffian blastema separate from protovertebræ and thick peritoneal epithelium. Hart. cam., ob. 3.

Plate VI.

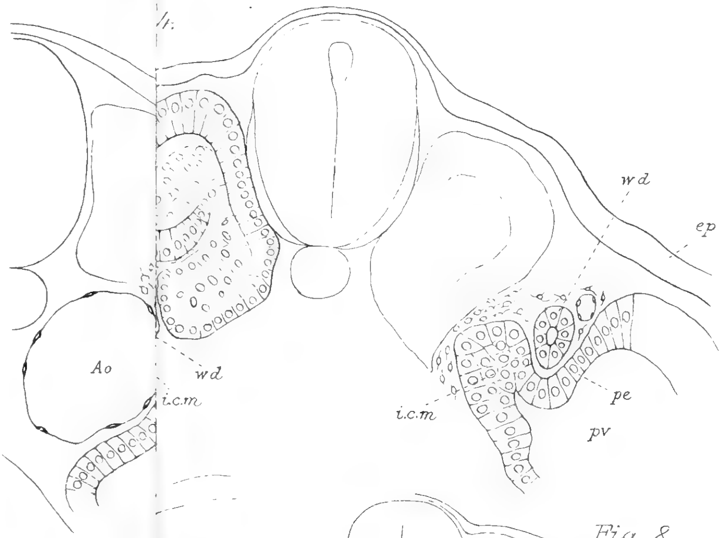


Fig. 5.

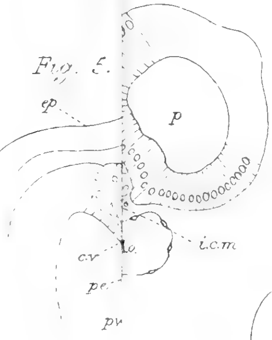


Fig. 8.

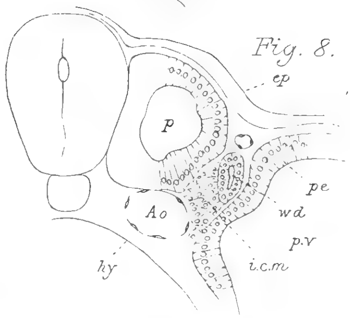


Fig. 9.

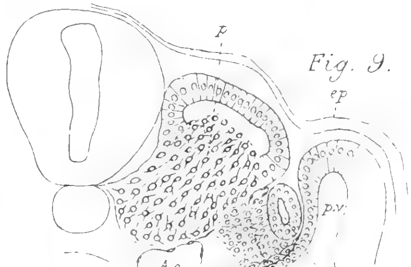


Fig. 18.

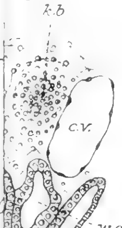


Fig. 10

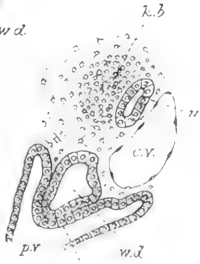


Fig 19.

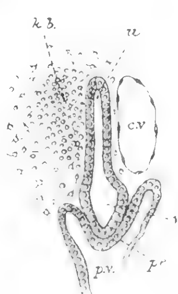


Fig. 20.

16.

A. Sedgwick del.

F. Huth, Lithr Edinr

F Bath lit.d Plat.

Fig. 21.

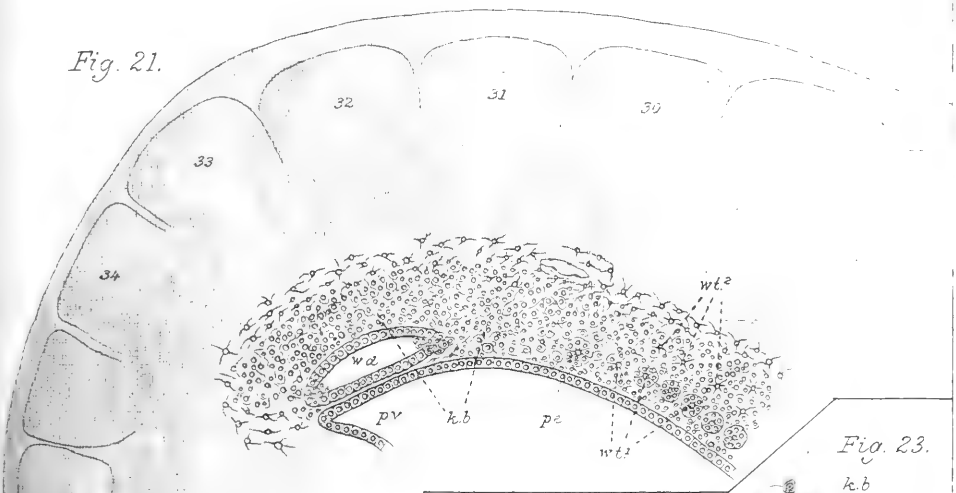


Fig. 23.

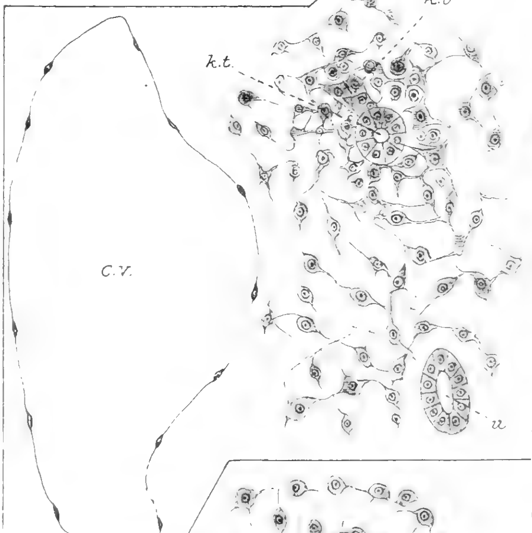
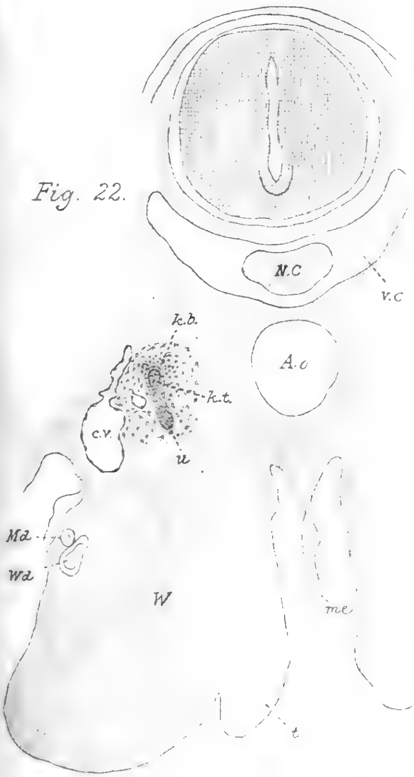


Fig. 22.



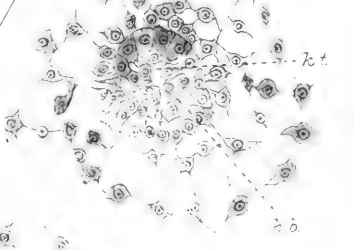


Fig. 24.

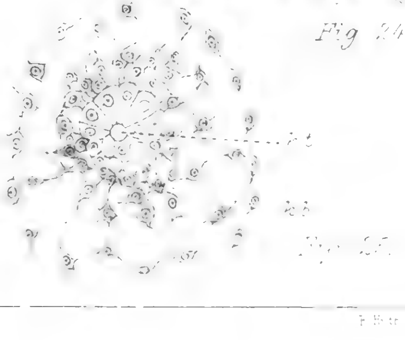


Fig. 25.

A. Sedgwick, del.

F. Huth, Lith^r Edin^r

Fig. 9.—Section through the twenty-fourth segment of a chick with twenty-nine protovertebræ, showing Wolffian blastema and thin peritoneal epithelium. Hart. cam., ob. 3.

Fig. 10.—Section through the twenty-ninth segment of a chick with thirty-four protovertebræ, showing the commencing development of a primary Wolffian tubule from Wolffian blastema. Hart. cam., ob. 4.

Fig. 11.—Section through a chick, end of third day or beginning of fourth, showing earliest appearance of a secondary tubule. Hart. cam., ob. 3.

Fig. 12.—Section through the thirty-second protovertebra of a chick with thirty-four protovertebræ, showing the kidney blastema.

Figs. 13—17.—A series of sections from the hind end of a chick of fourth day, illustrating the continuity of the Wolffian body with the cells forming the kidney blastema. Hart. cam., ob. 3.

Fig. 13.—Last section, in which a tertiary tubule was seen.

Fig. 14.—Last section, in which a secondary tubule was seen. The tubules in figs. 13 and 14 are contiguous.

Fig. 15.—Next section but one behind fig. 14.

Fig. 16.—Next section but one to fig. 15.

Fig. 17 a.—Section some distance behind that drawn in fig. 16.

Figs. 15, 16, and 17 show kidney blastema.

Fig. 17 shows opening of Wolffian duct into horn of cloaca.

Figs. 18—20.—Sections through a slightly older embryo than that from which above series was taken. Hart. cam., ob. 3. Showing (fig. 20), ureter opening into Wolffian duct, with shifted kidney blastema lying just internal to it.

Fig. 19.—Showing developing ureter and kidney blastema.

Fig. 20.—Section just anterior to ureter through the anterior end of the kidney blastema.

Fig. 21.—A longitudinal vertical section through the hind end of a four-day chick, showing continuity of kidney blastema with hindermost part of Wolffian blastema, in which the development of Wolffian tubule is taking place. No line of demarcation can be drawn between the two.

Fig. 22.—Section through a chick of seventh day or late in sixth, showing the portion of the ureter (*u.*) and its dorsal dilatation (*v. t.*) with regard to the Wolffian body (*w.*).

Figs. 23 and 24 are from sections of the chick from which fig. 22 was taken.

Fig. 23.—Section next but one to fig. 22. It shows the kidney tubule dorsal to the ureter, surrounded by the blastema.

Fig. 24.—Section next to fig. 23. It shows the dilated termination of the kidney tubule, and the continuity of its lining cells with those of the kidney blastema.

Fig. 25.—From a section through the kidney of an eight-day chick, showing the termination of a kidney tubule. It presents the same feature as fig. 24.

EXPLANATION OF PLATES VIII, IX, AND X,

Illustrating Mr. F. M. Balfour's Notes on the Development of the Araneina.

PLATE VIII.

Complete List of Reference Letters.

ch. g. Ganglion of cheliceræ. *c. l.* Caudal lobe. *ch.* Cheliceræ. *pd.* Pedipalpi. *pr. l.* Præoral lobe. *pp*[1]. *pp*[2]. *etc.* Provisional appendages. *p. c.* Primitive cumulus. *sp.* Spinnerets. *st.* Stomodæum.

I—IV. Ambulatory appendages. 1—6. Postoral segments.

Fig. 1.—Ovum, with primitive cumulus and streak proceeding from it.

Fig. 2.—Somewhat later stage, in which the primitive cumulus is still visible. Some distance from it is a white area, which is probably the rudiment of the procephalic lobe.

Fig. 3*a* and 3*b*.—View of an embryo from the ventral surface and from the side when six segments have become established.

Fig. 4.—View of an embryo, ideally unrolled, when the first rudiments of the appendages become visible.

Fig. 5.—Embryo ideally unrolled at the stage when all the appendages have become established.

Fig. 6.—Somewhat older stage, when the limbs begin to be jointed. Viewed from the side.

Fig. 7.—Later stage, viewed from the side.

Fig. 7*a*.—Same embryo as fig. 7, ideally unrolled.

Fig. 8*a* and 8*b*.—View of an embryo from the ventral surface and from the side, after the ventral flexure has considerably advanced.

Fig. 9.—Somewhat older embryo, viewed from the ventral surface.

PLATES IX AND X.

Complete List of Reference Letters.

ao. Aorta. *ab. g.* Abdominal nerve cord. *ch.* Cheliceræ. *ch. g.* Ganglion of cheliceræ. *ep.* Epiblast. *ht.* Heart. *hs.* Hemispherical lobe of supra-œsophageal ganglion. *l. l.* Lower lip. *m.* Muscles. *me.* Mesoblast. *mes.* Mesenteron. *mp. g.* Malpighian tube. *ms.* Mesoblastic somite. *œ.* Œsophagus. *p. c.* Pericardium. *pr.* Proctodæum (rectum). *pd.* Pedipalpi. *pd. g.* Ganglion of pedipalpi. *pr. c.* Primitive cumulus. *s.* Septum in abdomen. *so.* Somatopleure. *sp.* Splanchnopleure. *st.* Stomodæum. *su.* Suctorial apparatus. *su. g.* Supra-œsophageal ganglion. *th. g.* Thoracic ganglion. *v. g.* Ventral nerve cord. *yk.* Yolk. *y. c.* Cells derived from yolk. *y. n.* Nuclei of yolk cells.

I *g*—IV *g.* Ganglia of ambulatory limbs. 1—16. Postoral segments.

Fig. 10.—Section through an ovum, slightly younger than fig. 1. Showing the primitive cumulus and the columnar character of the cells of one half of the blastoderm.

Fig. 11.—Section through an embryo of the same age as fig. 2. Showing the median thickening of the blastoderm.

Fig. 12.—Transverse section through the ventral plate of a somewhat older embryo. Showing the division of the ventral plate into epiblast and mesoblast.

Fig. 13.—Section through the ventral plate of an embryo of the same age as fig. 3, showing the division of the mesoblast of the ventral plate into two mesoblastic bands.

Fig. 14.—Transverse section through an embryo of the same age as fig. 5, passing through an abdominal segment above and a thoracic segment below.

Fig. 15—Longitudinal section slightly to one side of the middle line through an embryo of the same age.

Fig. 16.—Tranverse section through the ventral plate in the thoracic region of an embryo of the same age as fig. 7.

Fig. 17.—Transverse section through the procephalic lobes of an embryo of the same age. *gr.* Section of hemicircular groove in procephalic lobe.

Fig. 18.—Transverse section through the thoracic region of an embryo of the same age as fig. 8.

Fig. 19.—Section through the procephalic lobes of an embryo of the same age.

Fig. 20 *a, b, c, d, e.*—Five sections through an embryo of the same age as fig. 9. *a* and *b* are sections through the procephalic lobes, *c* through the front part of the thorax. *d* cuts transversely the posterior parts of the thorax, and longitudinally and horizontally the ventral surface of the abdomen. *e* cuts the posterior part of the abdomen longitudinally and horizontally, and shows the commencement of the mesenteron.

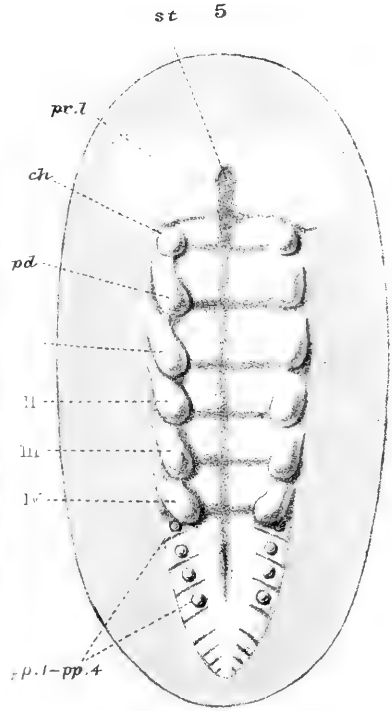
Fig. 21.—Longitudinal and vertical section of an embryo of the same age. The section passes somewhat to one side of the middle line, and shows the structure of the nervous system.

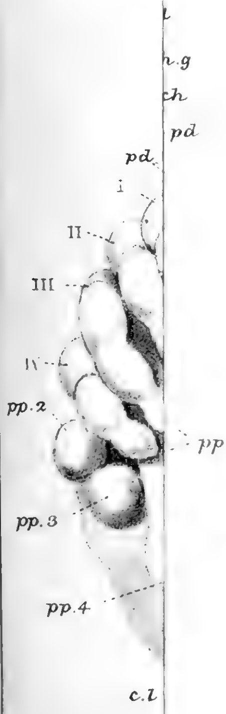
Fig. 22.—Transverse section through the dorsal part of the abdomen of an embryo of the same stage as fig. 9.

1

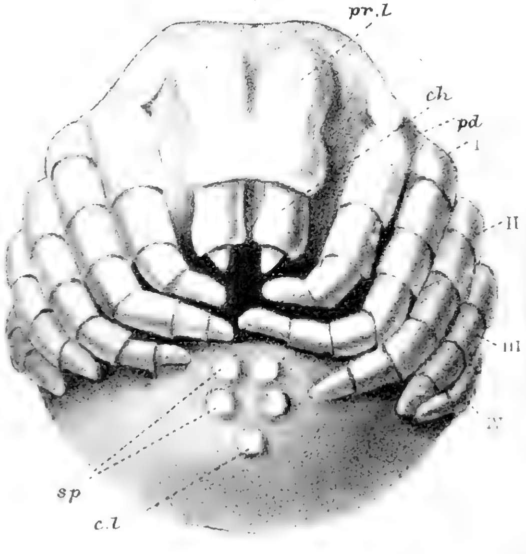
4

5





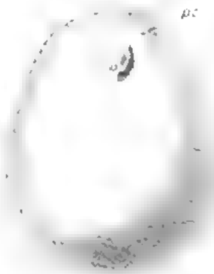
9



A.B. Balfour del. M

West, Newman & Co. imp.

1



2

3 a

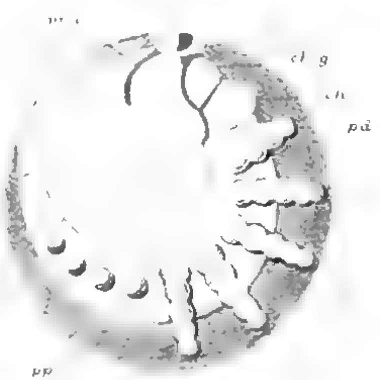
3 b

4

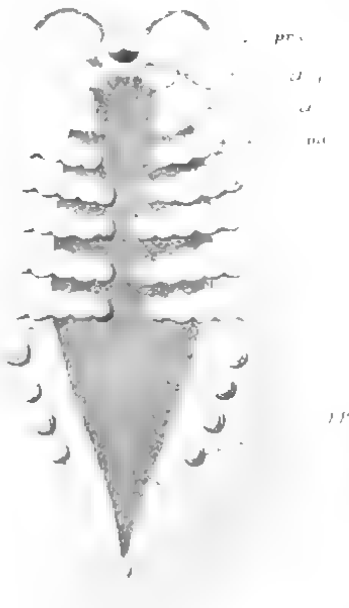
5

6

7



7 a



8 a

8 b

9

A.P. [illegible] del. M.P. Parker [illegible]

West Newman & Co imp.

Plate IX.

Fig. I

Fig. 15.

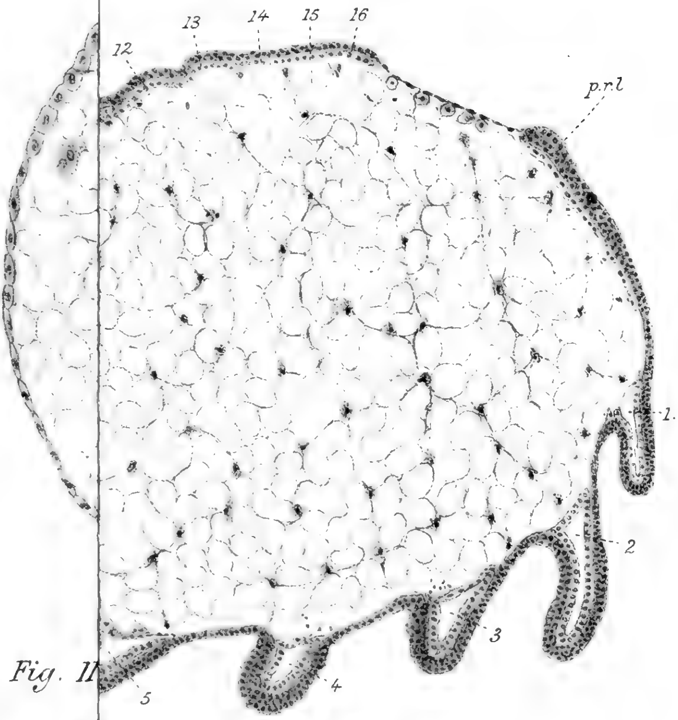


Fig. II

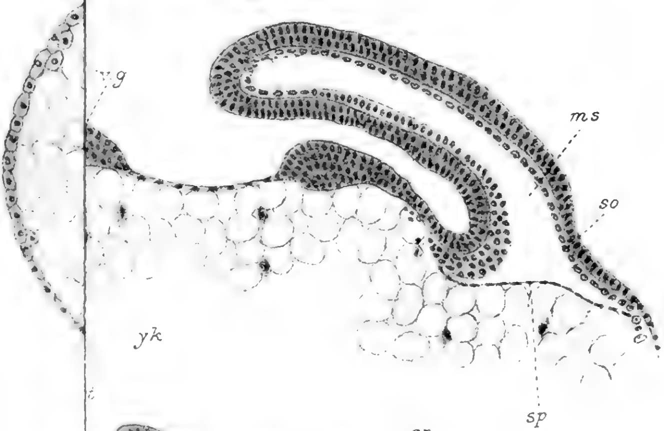
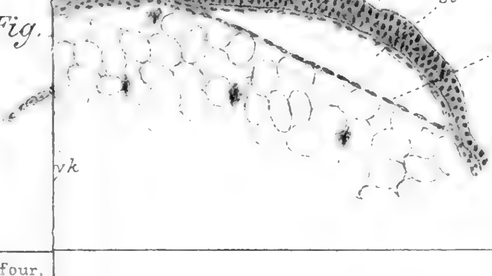


Fig.



F. M. Balfour,

F. Huth, Lith^r Edin^r

Fig. 8

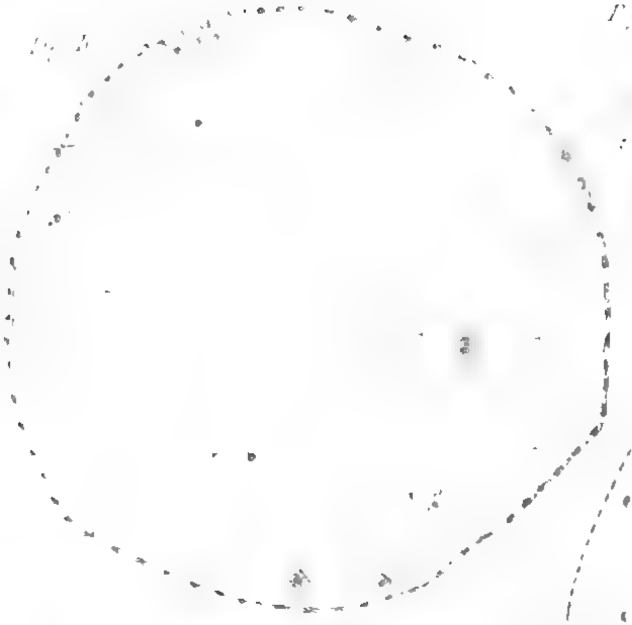


Fig. 9

Fig. 14

Fig. 15

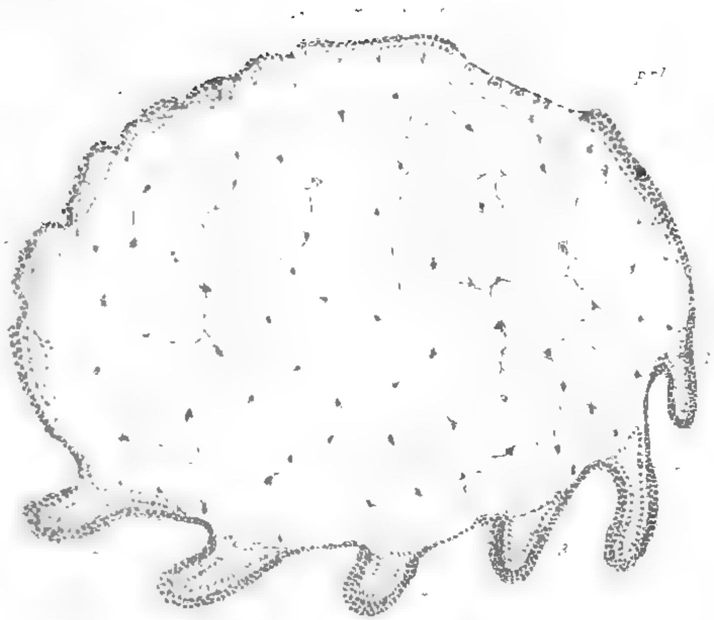


Fig. 11

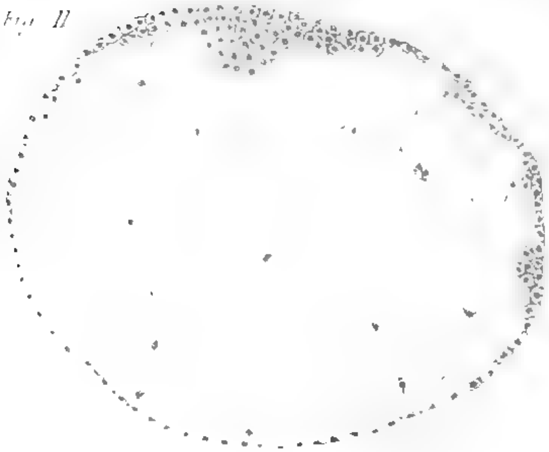


Fig. 10

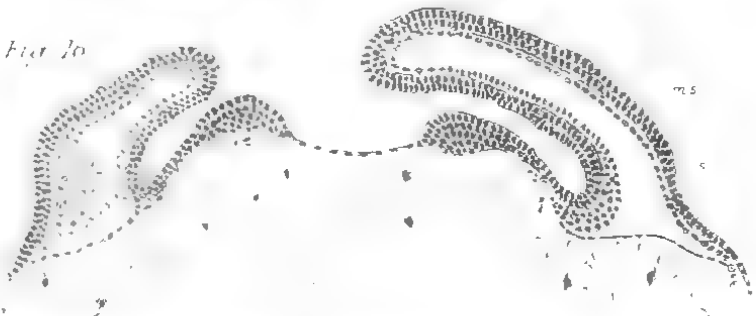
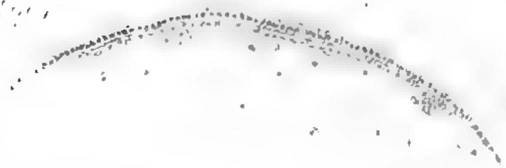


Fig. 7



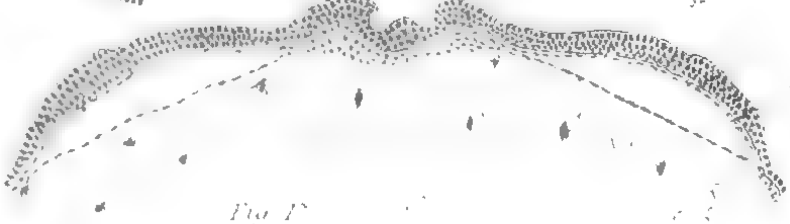


Fig. 12

F. Huth Lith^r Edin^r

Fig

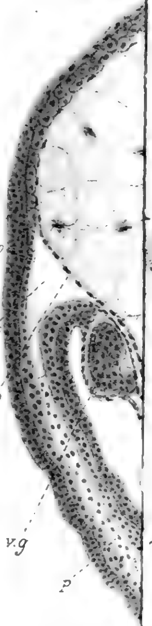


Fig. 19.

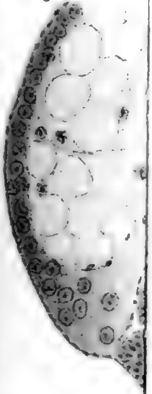
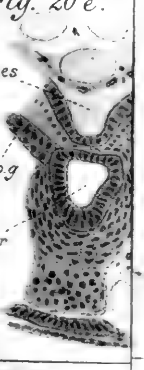


Fig. 20 e.



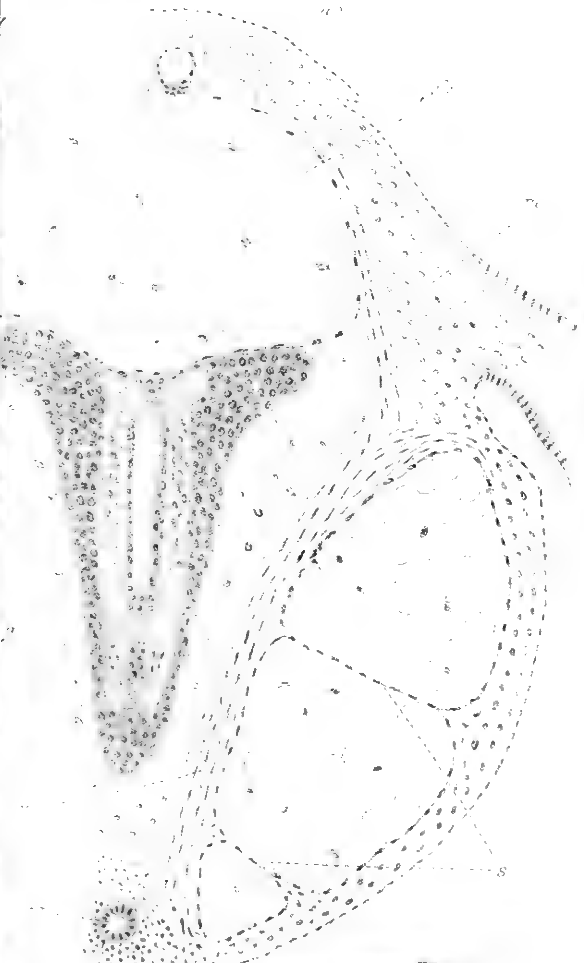
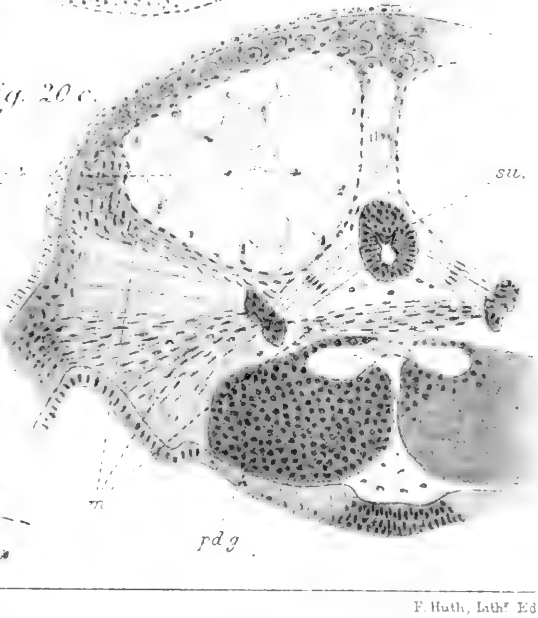
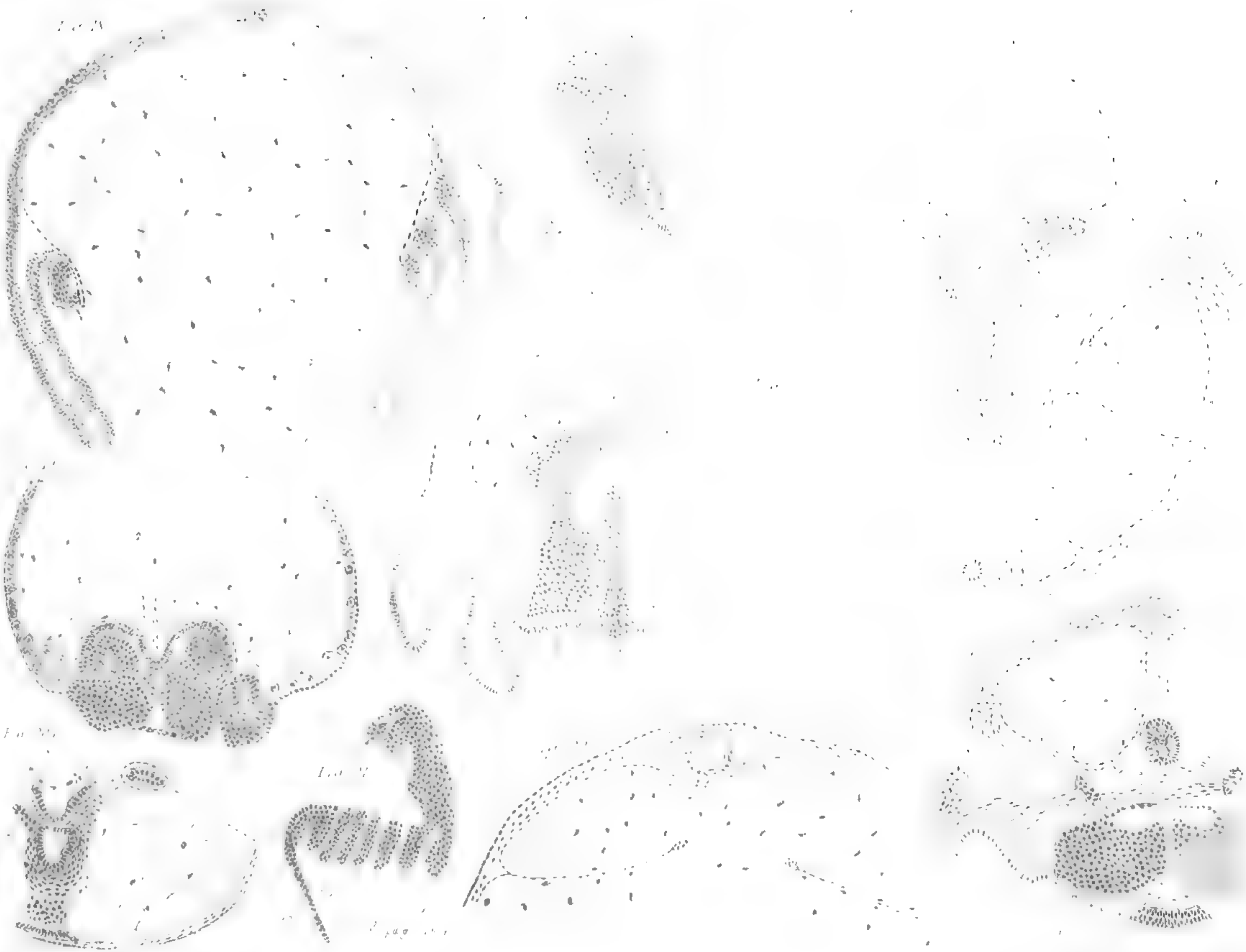


Fig. 20 c.



F. M Balfour, del

F. Huth, Lith^r Edin^r



STUDIES

FROM THE

MORPHOLOGICAL LABORATORY

IN THE

UNIVERSITY OF CAMBRIDGE.

EDITED BY

F. M. BALFOUR, M.A., F.R.S.,
FELLOW OF TRINITY COLLEGE, CAMBRIDGE.

PART II.

WILLIAMS AND NORGATE,
14, HENRIETTA STREET, COVENT GARDEN, LONDON
AND 20, SOUTH FREDERICK STREET, EDINBURGH.
1882.

LONDON:
PRINTED BY J. E. ADLARD, BARTHOLOMEW CLOSE.

CONTENTS.

N.B.—The papers marked with *one asterisk* are reprinted from the 'Quarterly Journal of Microscopical Science,' the papers with *two asterisks* are reprinted from the 'Proceedings of the Royal Society,' and the paper with *three asterisks* from the 'Proceedings of the Zoological Society.'

EXPLANATION OF PLATES I & II,

Illustrating Mr. Sydney J. Hickson's Memoir on the "Eye of Pecten."

FIG. 1.—A diagrammatic sketch of an eye of *Pecten maximus*. *a.* The cornea. *b.* The transparent basement membrane supporting the epithelial cells of the cornea. *c.* The pigmented epithelium. *d.* The lining epithelium of the mantle. *e.* The lens. *f.* The ligament supporting the lens. *g.* The retina. *h.* The tapetum. *k.* The pigment. *l.* The optic nerve. *m.* The retinal nerve. *n.* Complementary nerve. *p.* The circumpaleal nerve (Duvernoy). *q.* A supplemental nerve from pedal ganglion.

FIG. 2.—Epithelial cells of cornea.

FIG. 3.—Section through the junction of the pigmented epithelium with corneal epithelium.

FIG. 4.—Vertical section through eye of *Pecten maximus*. *a*, *b*. Cornea. *c.* Pigmented epithelium. *d.* Mantle epithelium. *e.* Lens. *g.* Retina. *h.* Tapetum. *k.* Pigment. *l.* Section of optic nerve.

FIGS. 5, 6.—Isolated rods. 6*a*.—Diagrammatic sketch of a central rod. *p. l.* Posterior limb. *m. p.* Membrane pierced by rods. *a. l.* Anterior limb. *s. r.* Spindle-shaped portion of rod. *n.* Nerves.

FIGS. 7.—Transverse sections through eye of *P. maximus*. *a.* Rods in section. *b.* Tapetum. *c.* Pigment. *d.* Retinal nerve.

FIG. 8.—Vertical section of the eye of *Pecten maximus*, showing the nerve dividing into retinal and complementary branches.

FIG. 9.—Vertical section of the eye of *Pecten maximus*, showing the termination of the retinal nerve. The retina has dropped out, and the frayed-out end of the nerve remains.

FIG. 10.—Section of eye of *Pecten opercularis*.

FIG. 11. Retina (*a*) of *P. opercularis*, (*b*) of *P. jacobæus*, (*c*) *P. maximus*.

Note.—A horizontal section means a section made in the same plane as the mantle. A transverse section, in a plane at right angles to the eye stalk. A vertical section, in a plane at right angles, both to the plane of the mantle and the last-named plane.

Plate I.

Fig 1

Fig 7

Fig 5

Fig 4.

Fig 6 a

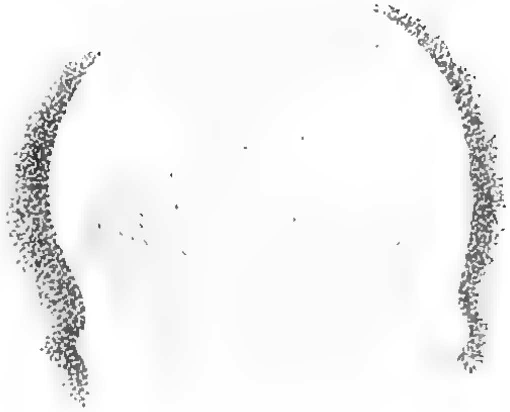


Fig. 9

Fig. 11

Fig. [illegible]

Fig. 8

The EYE *of* PECTEN. By SYDNEY J. HICKSON, B.Sc., Scholar of Downing College, Cambridge. (With Plates I and II.)

THE general absence of organs of vision amongst the members of the class Lamellibranchiata meets with a curious and interesting exception in the genera Pecten and Spondylus.

These genera have long been known to possess a great number of eyes of considerable complexity, situated on the border of the mantle. The number of these eyes varies considerably in different individuals, ranging in the genus Pecten from eighty to one hundred and twenty. Their position also varies; for, although they are always situated on the border of the mantle, yet sometimes they are placed at equal distances from one another, and sometimes they are clustered together in certain localities.

Notwithstanding this indefinite element, both in their number and position, which might be expected to run parallel with a primitive and simple organisation, their anatomy is exceedingly complicated, and exhibits all the most important structural elements of the eyes of the higher Vertebrata.

The earliest investigations into the anatomy of Pecten's eye are those of Krohn,[1] who gives a drawing of the course of the optic nerve. This drawing is copied in many of the subsequent papers on the subject by other investigators, and, as far as it goes, is correct. Duvernoy,[2] in his description of the nervous system of the Pectens, gives a short description of the anatomy of the eye. This paper, however, is chiefly valuable for the excellent figures and descriptions of the distribution of the nerves in the mantle, and the filaments which are given off from the main trunks of these to supply the tentacles and the eyes.

The researches of Blanchard[3] and of Keferstein[4] which followed did not add very much to our knowledge on this subject, and it was not until 1865 that any careful histological inquiries were carried on. It was Hensen[5] who first

---

[1] Krohn, 'Müller's Archiv,' 1840, p. 301, pl. xi.

[2] Duvernoy, 'Mémoires de l'Academie de Sciences,' t. xxiv, 1852. 'Mémoire sur le système nerveux des Acephalés,' p. 73, pl. ii.

[3] Blanchard, 'Organisation du regne animal: Mollusques Acephalés.'

[4] Kerferstein, 'Zeit. für wiss. Zoologie,' 1863, p. 133.

[5] Hensen, 'Zeit. für wiss. Zoologie,' 1865, p. 220.

gave figures of the characters of any of the histological elements. But as the eye of Pecten forms only a very small part of the paper, his figures and description are by no means complete, and in many respects they are incorrect. Finally, J. Chatin[1] has contributed two short papers, without figures, on this subject.

Of the scanty literature Hensen's paper is by far the most important, and he alone gives any good figures of sections of the eye, or of its elements; the other observers give remarkably few figures, and consequently I have had, owing to an imperfect knowledge of the German language, some difficulty in making myself acquainted with the substance of their papers.

I have been encouraged in publishing the following researches chiefly by this scarcity of good figures, but also because I believe, and will give my reasons for believing, that these eyes deserve more mention than is usually made of them in our zoological text-books.

My investigations were chiefly carried on upon *Pecten maximus*, but I have also had the opportunity of making sections of and studying the eyes of two other species, *Pecten jacobæus* and *Pecten opercularis*. The eyes of these three species differ from one another in one or two not altogether unimportant particulars, and, as I shall afterwards point out, they form an interesting gradation, the points of difference between *P. maximus* and *P. opercularis* passing through intermediate stages in *P. jacobæus*.

The eyes of Pecten maximus—are situated amidst a number of tentacles, which run all round the border of the mantle. These tentacles are capable of considerable movement, and frequently overhang the eyes and protect them from the light. The eyes themselves are situated upon short stalks, which resemble very closely the basal part of an ordinary tentacle.

This similarity caused Duvernoy to name a tentacle a tactile pedicel, and an eye an ocular pedicel, thus to a certain extent implying that they are morphologically homologous organs respectively modified for a tactile and an ocular function. This homology is justified by certain points in their anatomy, such as the course of the nerve and the arrangement of the muscular fibres, and I believe that when the development of these eyes is studied the homology will be still further confirmed.

The border of the mantle which bears the tentacles and

---

[1] J. Chatin, 'Bulletin de la Société Philomatique.' Paris, 1877.

eyes is covered with an epithelium, consisting of columnar, non-ciliated, and slightly granular cells bearing nuclei, situated near the base of the cells. As this epithelium passes over the eye-bulbs, it undergoes two interesting modifications. It becomes considerably thicker and filled with a dark brown pigment (Pl. I, fig. 1 *c*) as it passes round the sides of the eyes, but immediately in front of the eye (Pl. I, fig. 1 *a*), it again diminishes in thickness, and becomes perfectly transparent. By thus surrounding the eye on all sides with a dark-coloured pigment, leaving only a round spot in front, clear and transparent, the epithelium, by limiting the entrance of the light to a small diaphragm in front, here performs the function of an iris. The epithelium which runs over this transparent part, and which forms the epithelial layer of the cornea, differs from the ordinary epithelium covering the rest of the mantle in that their cells are rather larger, are perfectly transparent in the living condition, and the nuclei are large and spherical, and situated in the centre of the cells.

The eye consists of the following parts, which I shall now describe in order. The cornea, covered externally by its transparent epithelium, protects a large elliptical lens. Close up to the lens is the retina, but separated from it by the optic nerve, which spreads out over the anterior surface of the retina. The retina rests upon a tapetum, and behind this, occupying all the posterior concavity of the eye-cup, there is a red pigment.

The *cornea*—consists of two parts, the outer epithelium, which has already been described, and a basement membrane, consisting of a thin layer of connective tissue. As before stated, this epithelium is merely a modification of the general epithelium of this part of the mantle; and the pigmented epithelium surrounding the eye-bulbs (in like manner, a modification of the same tissue) is continuous with it all round its edge. The passage of the cells of the pigmented epithelium into those of the corneal epithelium is signalised by two important changes in the characters of the cells. In the first place the pigment entirely disappears, and the nuclei, which in the former case were obscured by the pigment, now become apparent, and in the second place the cells are considerably diminished in their longitudinal axis. The diminution in size of the cells causes the edge of the cornea to be sunk below the level of the pigmented epithelium; and a shallow trough runs round the line of its juncture with it (Pl. I, fig. 3). The convexity of the cornea is not great, and the dome of it frequently only just reaches the level of a line drawn from the highest points of the pigmented epithelium on either side of it. This appearance is not often seen in sections, as the pigmented epithelium rapidly shrinks, when the tissue dies, and under most reagents; but I am fully persuaded of the accuracy of this statement from an examination of the eyes of living specimens of *Pecten maximus* and sections of *Pecten opercularis.*

The delicate epithelial cells of the cornea, in consequence of being entirely unprotected by any membrane similar to the conjunctiva of the higher animals, are quite naked, and very liable to injury from the rough edges of the tentacles which surround them. The arrangement just described, however, probably prevents the tentacles from coming into immediate contact with them. The little trough which runs round the margin of the cornea always contains a little liquid, even when the eye itself is removed from the water; and the pressure of the tentacles when folding over the eye causes it to spread out as a thin layer over the cornea, and thus the cells are prevented from coming into immediate contact with the tentacle.

Thus, the two remarkable modifications, namely, the presence of a large quantity of pigment, and a greater longitudinal axis of the cells which the pigmented epithelium exhibits, are of considerable value to the eye, firstly, to prevent very divergent rays from entering, and secondly, to prevent any damage to the cornea caused by the rubbing of the adjacent tentacles over the sides of the eye.

The second layer of the cornea is about half as thick as the epithelial layer, and, like it, is perfectly colourless and transparent. It consists merely of a thin continuation of the connective tissue of the stalk. It may be called the basement membrane of the corneal epithelium, as from the absence of any definite cellular elements its only function probably is to support these cells.

Beyond the cornea this membrane becomes much thicker, and supports the pigmented epithelium, and at the same time structural elements make their appearance in it. From thence it passes into the connective tissue of the eye-stalk without further modifications.

The *lens*—is one of the most interesting parts of the eye. It is comparatively large, and is composed of a number of nucleated cells. In the fact that the lens is formed by more than one cell the eye of Pecten bears an interesting resemblance to that of the Vertebrata. The shape of the lens has been a subject of much dispute amongst the authors who have written on this subject. Krohn and Keferstein believed it to be spherical. Hensen has figured it filling up the space between the cornea and retina, and consequently of an irregular bi-convex shape.

It is difficult to see how a controversy on such a simple subject could have arisen, unless it is because different authors have examined different species, and described them for the genus.

As regards *Pecten maximus*, an examination of the fresh eye has convinced me that in this species the lens is elliptical, the major axis being parallel to the plane of the mantle. A section of the eye made in a plane at right angles to the plane of the mantle and the direction of its margin—that is, the plane which is most convenient for section-cutting, and the one which is apparently usually adopted—would consequently cause the lens to appear circular in section. In the diagrammatic representation of the eye (fig. 1) I have for convenience sake represented the lens as being at right angles to the plane of the mantle in order that the true shape of the lens may not be overlooked.

A fresh examination of the lens, when teased out from the rest of the eye, exhibits one or two interesting points. The lens is not, as in most eyes, perfectly colourless, but possesses a well-marked brown colouration, and a number of fine striæ may be seen running in the direction of the major axis. The lens does not appear so perfectly elliptical in the fresh condition as in certain sections I have made; it is drawn out somewhat longitudinally, so as to be more like a double cone than an ellipse. This is probably due to the lens being released from the ligaments and connective-tissue pressures, which cause it to retain its proper shape.

Hensen says that the lens is very soft, and the cells are light, polygonal, and nucleated. A careful examination of the lens of *P. maximus* has led me to a very different conclusion. The lens seemed to be of exactly the same nature as in the higher forms, and when teasing it out I found some difficulty in holding it with a needle, as it slipped away from under it when a slight pressure was exerted. As regards the shape of the cells composing the lens, they are not all polygonal, as would be inferred from Hensen's remarks on the subject. In the centre they are polygonal, but as they approach the periphery they become more and more flattened and elongated, until at the periphery they are strap-shaped. They are nucleated. As Hensen, I could find no membrane covering the lens, and no muscular fibres connected with it; but in a few cases I have observed a ligament, such as I have represented diagrammatically in fig. 1 *f*, which, I believe, forms a support for the lens. This ligament is usually broken by the action of reagents, and then hangs down by the side of the cavity, and thus becomes difficult to observe; at the same time the lens sinks down, and rests upon the anterior surface of the retina.

The lens is suspended in the space which corresponds with the vitreous humour in the higher animals. This space is filled with an aqueous humour in Pecten. The lens is larger, and, consequently, the space occupied by aqueous humour relatively smaller in *P. maximus* than it is in either *P. jacobæus* or *P. opercularis*, and in *P. jacobæus* it is larger than in *P. opercularis*.

The *retina*—does not line the concavity of the eye-cup, as it does in most well-developed eyes, but is nearly flat, and a considerable space is left between it and the floor of the cup, which is filled up by the red pigment. In consequence of this the retina appears in section to be a thick band crossing the eye from side to side. Thus, just as the lens was remarkable for the way in which it approached the retina by hanging back into the cavity, so the retina is remarkable for the manner in which it leaves the posterior concavity of the eye-cup to approach the centre. The eye of Pecten, in fact, presents the interesting peculiarity of the approach of the lens and the retina towards the centre, so that in *P. maximus* they almost touch.

The anterior surface of the retina is convex at the sides and concave in the middle, but these convexities and concavities vary in different species. The different layers of the retina will be described from behind forwards, as it will be easier to trace the transitions in that way than if described from before backwards. They are—1°. Posterior limbs of the rods. 2°. Anterior limbs of the rods. 3°. Spindle-shaped nucleated rods. 4°. Molecular and nuclear layer. 5°. Nerves.

The posterior limbs of the rods stand upon a membrane, which runs along the posterior side of the retina; at their anterior ends they pierce a very delicate membrane, and pass into the anterior limbs of the rods. The anterior limbs are about twice as long as the posterior limbs, and are usually smaller in diameter, and situated farther apart than the posterior limbs. That they are circular in section may be seen from Pl. II, fig. 7*a*, which is a drawing of a section made at right angles to the eye-stalk. The anterior limbs of the rods are sometimes swollen so as to appear oval; this condition occurs especially in the rods at the side convexities. Fig. 6 represents an isolated rod in this condition.

The anterior ends of the rods contract considerably, and again expand into spindle-shaped bodies, each of which contains a nucleus; so that in *P. jacobæus*, where the retinal elements of this region are difficult to distinguish, there may be seen a single row of nuclei running from end to end of the retina, and following its sinuosities (Plate II, fig. 11 *b*).

In some of the rods at the side of the retina a second spindle-shaped body follows the first one, as represented in the isolated rods in figs. 5, 6, but usually the anterior end of the spindle is drawn out into a delicate thread, which occasionally possesses nuclear swellings. Finally, this thread breaks up into a network, which bears a number of nuclear-like bodies at its nodes, and several round molecular bodies appear to be caught in its meshes. These bodies are so much like the ordinary nuclei of the network that I am inclined to believe that they are, in reality, merely modifications of them, and in some way connected with the network (fig. 6 *a*). Anteriorly the fibres of the network bend at right angles and enter the nerve layer, which covers the anterior surface of the retina. This nervous layer will be described with the description of the optic nerves.

The above is a description of the retina as I found it in *P. maximus*, and I believe it holds good for the other members of the genus. The elements of the retina are so much larger in this species, and the spaces between the rods and network, &c., so much more considerable, that it is a great deal easier to investigate; but I believe careful examination of the other species would show that they do not differ from this in any important detail.

The *tapetum*—is placed immediately behind the retina, and may help in its support. When fresh,[1] the tapetum exhibits a display of colours, and it is this membrane which gives the eyes their beautiful metallic lustre. When examined with a $\frac{1}{5}$th-inch obj. it seems to be composed of a great number of little black specks separated by a fine yellow membrane, but careful examination with a higher power shows that it is composed of a great number of fine fibrils crossing at right angles.

The space between the tapetum and the posterior part of the eye-cavity is filled with a red fluid *pigment*. In the fresh condition the pigment readily flows on to the slide when the eye is pricked, but in sections of the eye which has been

---

[1] I have one series of sections stained in osmic acid, and mounted in Canada balsam, which has retained this display of colours.

hardened by alcohol or other reagents the pigment adheres to the tapetum or posterior wall of the eye-cup.

Hensen figures a layer of cells in this position, but I have never been able to observe anything of the kind; the pigment contains no cellular elements at all, nor is there a layer of cells lining the cavity which contains the pigment. The pigment consists of a number of bright red granules floating freely in a colourless fluid.

The *nervous supply*—of the eye of Pecten is perhaps the most interesting of the many peculiarities of this eye. The nervous system of Pecten is well described by Duvernoy in the paper referred to above. The mantle is supplied by a number of branches given off from the principal ganglia. These branches all fall into a large nerve, which runs round the margin of the mantle, and which Duvernoy calls the "circumpalial" nerve. This nerve is figured in section in fig. 1, Pl. I, one of the nerves joining this nerve being figured at fig. 1, *q*. This "circumpalial" nerve gives off filaments to supply the tentacles and eyes.

Krohn first gave a drawing of the optic nerve, and described it as a single nerve passing off from this trunk, and dividing into two branches as it aproaches the eye. Later observers have, however, drawn and described two nerves passing off from the "circumpalial" nerve. My researches have led me to believe that Krohn is right, and that such a figure as Hensen gives in his paper, representing two main trunks passing up to supply the eye is erroneous. Plate II, fig. 9, of *P. maximus*, shows the division of the single nerve into its two branches. In fig. 1 the course of the optic nerve, before its division into two branches, was carefully drawn from one of a complete series of sections, and in none of the other sections could I find a trace of any other nerve proceeding from the "circumpalial." The branching of the nerve takes place in a plane at right angles to the plane of the mantle. When the optic nerve approaches the eye it divides into two branches, which may be called the "retinal nerve" and the "complementary nerve." The former passes up the side of the eye cavity, and spreads over the anterior surface of the retina; the latter soon loses its sheath, and divides up into a number of branches, which supply the tissues surrounding the eye. The course which the retinal branch takes may be seen in Pl. I, fig. 1, and in Pl. II, figs. 8 and 9. In figs. 8 and 9, the first section is cut through the optic nerve, and shows the manner in which the retinal branch runs up the side of the eye-cavity; the second section shows the manner in which the branch bends over on to the retina and spreads out. The distribution of the complementary branch is diagrammatically represented in fig. 1 *n*; it seems to divide into a number of branches which envelope the eye-cup, and probably send filaments to the cornea, lens, tapetum, and epithelium.

Comparison of the eyes of the three species, *P. maximus, P. jacobæus,* and *P. opercularis.*—The eye of *P. maximus* is undoubtedly the most highly developed, the eye of *P. opercularis* is the simplest, whilst *P. jacobæus*, although more like *P. opercularis* than *P. maximus,* shows many points in which it is intermediate between the two.

The lens in *P. opercularis* is separated from the retina by a considerable space (Pl. II, fig. 10), and consequently the chamber containing the humour is relatively large. In *P. jacobæus* the lens is larger than in *P. opercularis,* and the chamber consequently smaller; and in *P. maximus* the lens is very large, and nearly touches the retina, the chamber of the eye being sometimes very small. A gradation is thus observed in the character of this part of the eye in the three species. In *P. maximus* but a small space is filled with humour, in *P. jacobæus* a much larger space is filled with it, and in *P. opercularis* there is a larger space still.

Again, when the retinas of the three species are compared, a similar gradation is found. The retina of *P. opercularis* is comparatively thin, and the concavity and convexities of its anterior surface slight. In *P. jacobæus* the retina is decidedly thicker, and the anterior surface is more convex at its sides than in *P.opercularis ;* moreover, it may be noticed that the delicate membrane which separates the anterior from the posterior limbs of the rods has become bent up in the regions corresponding with the anterior convexities of the retina. In *P. maximus* all these variations become much exaggerated. The retina is much thicker than in either of the other species; and the side convexities of its anterior surface are much bolder (Pl. II, fig. 11, *a, b, c*). The anterior concavity does not undergo much variation.

The shape of the membrane separating the anterior and posterior limbs of the rods is greatly altered. In *P. opercularis* this membrane is observed, in section, to stretch from side to side without any well-marked curves; in *P. jacobæus* two well-marked curves, corresponding with the anterior convexities of the retina, are observed; but in *P. maximus* these curves are converted into two distinct folds, which run up into the substance of the retina. The membrane between the folds does not sink again as low as it is at the commencement of the folds, and consequently the central part of the retina is raised in the form of a table above the level of its sides. This elevation of the central part of the retina may be also seen in *P. jacobæus*, though it is not nearly so well marked. The folds which occur in *P. maximus* cause the rods to appear to be given off in a pinniform manner at the sides of the retina, and before I found the intermediate condition in *P. jacobæus* I had some difficulty in determining the true relationship between the retinas of *P. maximus* and *P. opercularis*. (Compare *a, b, c,* fig. 11).

In addition to those just mentioned there are other minor points in which the eyes of these species differ from one another, such as in the shape of the cells composing the lens and in the distribution of the retinal nerve, &c., but they are comparatively slight.

General considerations.—Having thus described, in some detail the anatomy of the various parts which compose the eyes of Pecten, I shall, before leaving the subject, point out some of their interesting morphological peculiarities. It is, in itself, a remarkable thing to find a large and variable number of eyes situated on an area at some considerable distance from any central nerve-ganglion; and, when it is remembered that the class and even family (with one other exception, *e. g.* Spondylus) to which the genus belongs, possess no organs of vision at all in the adult condition, it is altogether surprising that they should be of such extraordinary complexity as they have proved to be. The high structural development that this eye has attained is, however, not so remarkable as the fact that in many ways it differs from the ordinary Invertebrate eye, and resembles that of the Vertebrata.

In the first place, the lens is built up of a large number of distinct nucleated cells, which undergo a flattening at its circumference very similar to that found in the eye of the Vertebrata. Whether the lens is developed from the cells of the epiblast, as in the Vertebrata, or from the mesoblast, must at present be left unsettled, but it will probably be found, when the development of the eye is studied, that in this respect also it resembles the eyes of the Vertebrata. The tapetum, a structure which is of considerable importance to animals which are nocturnal or aquatic in habit, has hitherto been described only in the Vertebrata. That Pecten possesses a tapetum as highly developed as any found amongst the Vertebrata is anatomically a point of considerable interest; but it also indicates to a certain extent the physiological capability of the eye.

The chief interest, however, lies in the relative positions of the optic nerve, the retina, and the pigment. In the eyes of the Cephalopods the pigment layer is situated in front of the rods, and the nerve-fibres enter the rods from behind. In the eyes of the Gasteropoda, the Crustacea, &c., down to the simplest form of eye, such as that of the Rotifera, the same relationship of these parts holds good. In the Vertebrata, however, their relative positions are reversed; the optic nerve pierces the retina, and distributes itself over the front of the retina, whilst the pigment is situated behind it. In Pecten the relationship of these parts is the same as that in the Vertebrata; the nerve passing up the side of the eye-cup bends over, and spreads itself over the anterior surface of the retina. The pigment also is situated behind the retina. Pecten is not, however, the only Invertebrate whose eyes are built up on this type. Semper[1] has recently pointed out that on the backs of certain slugs (Onchidium) a number of eyes are found, and that in these the nerves pass to the front of the retina before being distributed. On account of this distribution of the optic nerve he says that they belong to the Vertebrate type of eye (typus der Wirbelthieraugen), so that two animals are now known, each belonging to a large and important class of Invertebrata (Gasteropoda and Lamellibranchiata respectively) that possess eyes which are built up on this type. The eyes of Pecten are even more deserving of the name of Wirbelthieraugen than those of Onchidium, for they are much more highly developed, and possess, in addition to this relationship of the nerve and retina, other Vetebrate peculiarities. The lens is multicellular, a character which, although not unknown amongst the Invertebrates, is much more characteristic of the Vertebrata. The tapetum, too, a structure which doubtfully exists in any other Invertebrata is found in Pecten and some Vertebrates. But, although the application of this word Wirbelthieraugen to these eyes is convenient for the adult condition, it must be carefully remembered that the development of these eyes is essentially different from that of the Vertebrate eye. The Vertebrate eye is formed in the embryo from a hollow process given off from the brain, and the future eye-cup is formed by an invagination of this process. It is impossible for the eyes of Pecten or Onchidium to be formed by any process similar to this. Thus, in the young state these eyes are essentially different from those of the Vertebrata, and the resemblance

---

[1] Semper, 'Uber sehorgane vom Typus der Wirbelthieraugen auf dem Rücken der Schnecken.' Wiesbaden, 1877.

in the adult is merely accidental, and by no means due to morphological identity.

Little is known and little can be said concerning the function of the eyes of Pecten. The presence of such a well-formed tapetum makes it probable that they are capable of appreciating very diffused light, and the close approximation of the lens to retina makes it exceedingly improbable that any image is formed upon the latter.

A few experiments have been made on the extent of their visual power, which make it very doubtful whether they are of much value to the animal in avoiding its enemies. The most reasonable theory of their function seems to be that, when on the ebbing of the tide, a probability arises that they will be left high and dry on the shore, they can appreciate the fact by the growing intensity of the light, and, by that peculiar flapping motion of their valves the Pectens are so remarkable for, move away into deeper water.

These researches were entirely carried on in the morphological laboratory of the University of Cambridge, and my best thanks are due to Mr. Balfour for his valuable advice and encouragement during the whole course of my researches. Owing to his kindness, also, I have been enabled to examine some of Semper's preparations of the eye of Onchidium, to which reference has been made in the text.

Methods.—For a general examination of the eye the best method is to harden in alcohol and stain by immersion in hæmatoxylin for twenty-four hours. Of the osmic-acid acid preparations the best were obtained by immersion in a 1 per cent. solution for fifteen minutes, followed by absolute alcohol for three or four days. This method is of great value for studying the retina and lens. I have also used gold chloride for staining the nerves with some success. For examining the tapetum the best preparations I have were made from some eyes given me by Mr. Haddon, which had been treated with picric acid. This reagent seems to have dissolved away the red pigment, and consequently left the tapetum free from the numerous little red granules which generally cling to it. For examining the isolated rods of the retina I have allowed the eyes to remain in a solution of chloral hydrate for four or five days. I have then dissected out the retina with needles as carefully as possible, and poured a drop or two of hæmatoxylin on to the slide. When the retina had been standing in hæmatoxylin in this manner for some hours it was washed with water, teased out with fine needles, and mounted in glycerine.

DESCRIPTION OF PLATE III,

Illustrating Mr. Adam Sedgwick's Paper "On the Early Development of the Anterior Part of the Wolffian Duct and Body in the Chick, together with some Remarks on the Excretory System of the Vertebrata."

List of Reference Letters.

al., alimentary canal; *ao.*, aorta; *c. v.*, cardinal vein; *e. gl.*, external glomerulus; *ep.*, epiblast; *hy.*, hypoblast; *i. c. m.*, intermediate cell mass; *i. gl.*, internal glomerulus; *k. b.*, blastema of Wolffian tubules; *me.*, mesentery; *m. p.*, muscle plate; *nc.*, notochord; *p. c.*, body cavity; *p. f.*, peritoneal funnel; *pv.*, proto-vertebra; *pv.*^{1}, cell-mass, which later becomes a protovertebra; *W. d.*, Wolffian duct; *W. t.*, Wolffian tubule.

Fig. 1.—Section through 10th segment of a chick with ten segments, showing origin of Wolffian duct.

Fig. 2.—Section through 10th segment of a chick with twelve segments. Shows second stage in development of Wolffian duct.

Figs. 3 and 4.—Successive sections through the 10th segment of a chick with thirteen segments. Shows further development of Wolffian duct.

Fig. 5.—Section through 10th segment of a chick with fourteen segments, showing further development of Wolffian duct and anterior Wolffian tubules.

The above series are all taken through the points where rudimentary segmental tubes connect the Wolffian duct and peritoneal epithelium, except Fig. 4, which is through a point between two tubules. The object of the series is to trace the continuity in the development of the Wolffian duct and anterior tubules, which exists between the 7th and 11th segments inclusive.

Fig. 6.—Section through a chick with twelve segments just behind the 12th segment. Shows independence of Wolffian duct from peritoneal epithelium and intermediate cell mass.

Fig. 7.—Section through the 13th segment of a chick with thirteen segments. Shows how almost at once the Wolffian duct becomes connected with the intermediate cell mass. The continuity between the two structures is not well represented in this figure.

Fig. 8.—Section through 16th segment of a chick with twenty-one segments. Shows separation of Wolffian duct and intermediate cell mass, which persists for some time in this region.

Figs. 9 and 10.—Successive sections through the 15th segment of a chick with about twenty-two protovertebræ, showing the connection between the Wolffian duct and intermediate cell mass. In Fig. 9 the intermediate cell mass is continuous with the peritoneal epithelium; in Fig. 10 it is separate.

DESCRIPTION OF PLATE III—*continued.*

Fig. 12.—Section through a chick late in the third day behind the 16th segment, showing the independence of the developing Wolffian tubule and the Wolffian duct in this region.

Figs. 13, 14, and 15.—A series of successive sections through the 13th segment of a chick with thirty-one or thirty-two segments, Fig. 13 being anterior. Show a further stage in the development of a Wolffian tubule in this region. In Figs. 13 and 14 the tubule is connected to the peritoneal epithelium, and a lumen has appeared in it, which is continued behind into the part of the tubule separated from the peritoneal epithelium, seen in Fig. 15.

Figs. 16, 17, and 18.—Sections through the 13th or 14th segment of a chick with thirty-four or more segments. Show the further development of a Wolffian tubule in this region, and the first appearance of the external and internal glomeruli. Figs. 16 and 17 are contiguous sections. Between Figs. 17 and 18 there is a section not figured. The three figures respectively correspond to and are further developments of Figs. 13—15.

Figs. 19, 20, and 21.—Successive sections through the 13th or 14th segment of a chick with thirty-six or more segments. Show further development of external glomerulus.

Fig. 22.—Diagrammatic longitudinal, vertical section, showing the relations of the external and internal glomerulus.

Fig. 23.—Section through the 13th or 14th segment of a chick with thirty-three segments, showing the opening of the Wolffian duct near the external glomerulus.

Fig. 24.—Section through the anterior part of the Wolffian body of a 4th day chick, showing the glomerulus projecting into the Wolffian duct.

Fig. 25.—Section through the hinder region of a tadpole of *Rana temporania,* showing the first appearance of the cells from which the Wolffian tubules will arise.

Plate III.

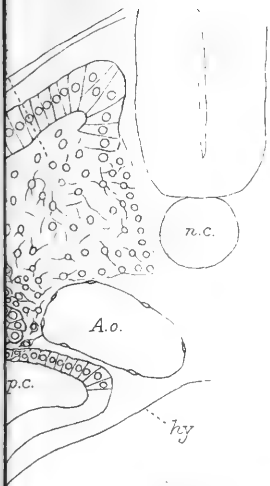
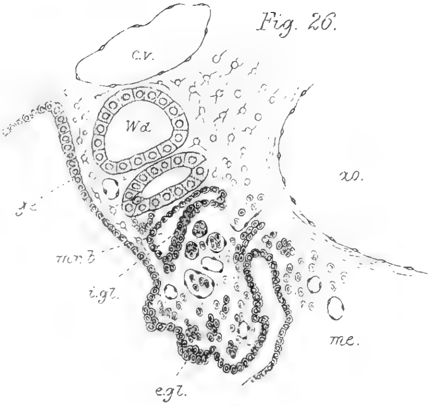


Fig. 26.



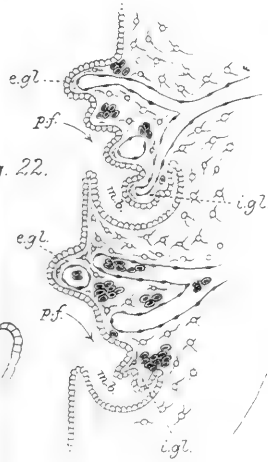
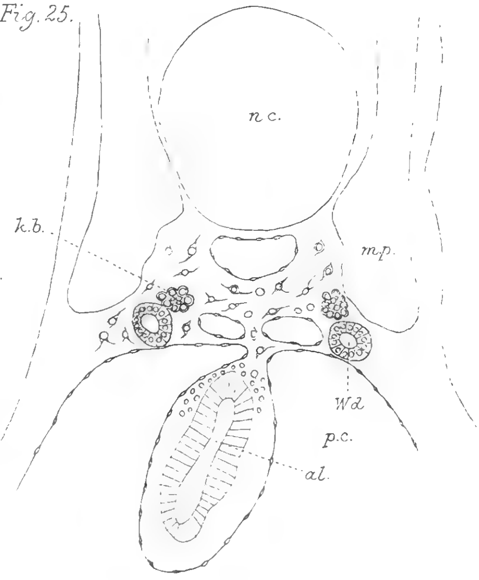


Fig. 22.

Fig. 25.



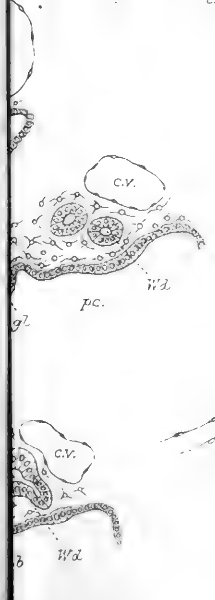
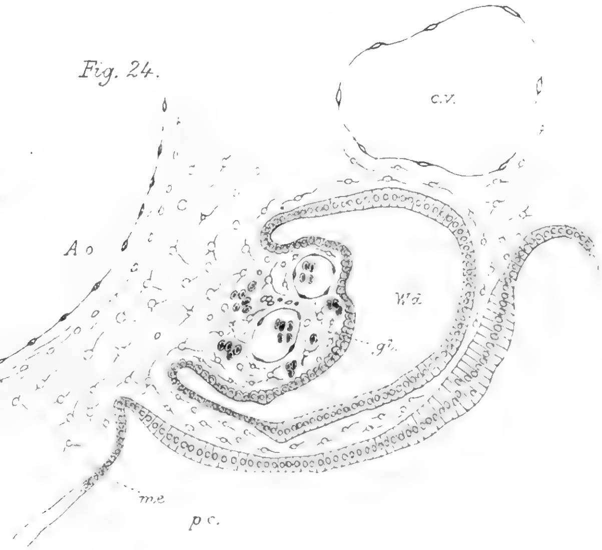


Fig. 24.



On the EARLY DEVELOPMENT *of the* ANTERIOR PART *of the* WOLFFIAN DUCT *and* BODY *in the* CHICK, *together with some* REMARKS *on the* EXCRETORY SYSTEM *of the* VERTEBRATA.

By ADAM SEDGWICK, M.A., Fellow of Trinity College, Cambridge. With Plate III.

THE following paper is divided into two parts. The first part contains an account of observations on the development of the Wolffian duct and anterior Wolffian tubules in the chick, being supplementary to my paper on the "Kidney of the Chick."[1] The second part is devoted to a discussion of the vertebrate excretory system in general.

I. *Early Development of the Wolffian Duct and Anterior Wolffian Tubules in the Chick.*

The first trace of the Wolffian duct is visible in an embryo with eight protovertebræ as a slight projection from the intermediate cell mass towards the epiblast in the region of the 7th and 8th protovertebræ. The projection also extends back behind the region of the protovertebræ for a short distance. In a chick with nine or ten protovertebræ a similar condition is found, *i.e.* a projection from the intermediate cell mass towards the epiblast in the region of the 7th, 8th, 9th, and 10th protovertebræ, and for a short distance behind the region of the protovertebræ.

In a chick with ten protovertebræ the projection is beginning to show signs of separation from the intermediate cell mass at certain points. The appearance presented by the rudiment of the Wolffian duct in the 10th segment of a chick with ten segments is shown in fig. 1.

In a chick with eleven protovertebræ the rudiment of the Wolffian duct is still present as a projection from the intermediate cell mass in the region of the 7th, 8th, 9th, 10th, and 11th protovertebræ; but behind the region of the protovertebræ it has grown back for a short distance between the epiblast and mesoblast as an irregular cord of cells not connected to the peritoneal epithelium. A partial separation of the Wolffian duct from the intermediate cell mass is now effected in the region of the 7th to the 10th protovertebræ. This separation

---

[1] "Development of the Kidney in its relation to the Wolffian Body in the Chick," 'Quart. Journ. Mic. Sci.,' vol. xx.

is not, however, complete; but *the Wolffian duct remains connected to the peritoneal epithelium at certain intervals by short cords of cells.*

In a chick with twelve protovertebræ the separation of the Wolffian duct from the intermediate cell mass in the region of the 7th to the 11th protovertebræ inclusive is as complete as it ever will be, *i.e.* it has separated for the greater part of its length, but remains attached to the peritoneal epithelium at certain points, by cords of cells (fig. 2) derived from the cells of the intermediate cell mass connecting the rudiment of the Wolffian duct with the peritoneal epithelium. These cords of cells are the commencing Wolffian tubules of the anterior part of the Wolffian body, and are more numerous than the segments in which they are placed. Behind the region of the protovertebræ in a chick of this age (twelve protovertebræ), the Wolffian duct has grown back as an irregular cord of cells (fig. 6), independent of the intermediate cell mass, for a short distance, thus repeating the feature of the last and succeeding stages in this particular. In the region of the last (12th) protovertebra, however, the cord of cells constituting the Wolffian duct at this stage is now continuous with the intermediate cell mass at certain intervals. Comparing the sections through the 12th segment of this stage with those just behind the 11th protovertebra of the previous stage, it is seen that the Wolffian duct has enlarged, and by a downgrowth of cells from it, with which probably is connected an upgrowth from the intermediate cell mass, has become in certain places connected with the intermediate cell mass. These secondary connections constitute the commencing tubules of this part of the Wolffian body.

In a chick with thirteen protovertebræ an advance precisely similar to that characterising the previous stage has taken place, *i.e.* the Wolffian duct has become connected with the intermediate cell mass in the 13th segment (fig. 7), and behind this point is free from adjacent structures.

In a chick with fourteen or fifteen protovertebræ the process of development remains the same. So that in a chick with fifteen segments the following is the condition of the Wolffian duct:—It extends from the 7th to the 15th segment as a solid cord of cells, connected at intervals with the peritoneal epithelium by the commencing Wolffian tubules; behind the 15th segment it extends for a short distance as a free cord. The further development differs from that just recorded in this important particular; the duct does not become connected with the intermediate cell mass of the newly-formed last segment, but remains separate for a considerable interval of time (till towards the end of the third day) from it. In other words, the formation of the Wolffian tubules and their connection with the Wolffian duct is deferred behind the 15th segment.

To sum up the developmental changes above recorded, the Wolffian duct arises as a continuous ridge of cells projecting from the intermediate cell mass towards the epiblast in the region of the 7th to 11th protovertebræ inclusive. This ridge separates from the intermediate cell mass from before backwards, remaining, however, connected with it at intervals by the rudimentary Wolffian tubules. Meanwhile, from the hind end of it there grows back a cord of cells independent at first of the adjacent structures, but immediately on the formation of the hinder segments becoming connected with the intermediate cell mass of each segment in turn. This happens as far back as the 15th segment; behind this point it grows back as a solid cord, which does not become connected with the intermediate cell mass until the tubules of the Wolffian body have made considerable advance in their development.

Figs. 1—7 are meant to illustrate the above method of development. Figs. 1—5 are from the 10th segment of chicks, with ten, twelve, thirteen, and fourteen protovertebræ respectively. They are all taken through points where the Wolffian duct remains attached to the peritoneal epithelium, *i.e.* through a rudimentary tubule, excepting fig. 4, which is from a section close to fig. 3, and shows the condition of things in one of the intervals between the points of continuity.

Fig. 6 is taken from a section just behind the last segment of a chick with twelve segments, and shows the complete independence of the Wolffian duct.

Fig. 7 is from the 13th segment of a chick with thirteen segments, *i.e.* from the same region as fig. 6, and it shows the connection which has become established between the Wolffian duct and the intermediate cell mass by a mutual growth of these structures.

Fig. 8 is from the 16th segment of a chick with twenty-two protovertebræ, and is illustrative of the fact derived from an inspection of all the sections of the segment, that the Wolffian duct is independent of the peritoneal epithelium. From the 15th segment the Wolffian duct grows back independently to the cloaca, into which it eventually opens, and a lumen appears in it from before backwards.

In fig. 11, taken from a chick at the end of the third day, it is still distinct from the now considerably developed Wolffian tubule (*w.t.*).

For purposes of description I shall divide the Wolffian body into three regions—(1) The part found within the limits of the 7th—11th segments inclusive; (2) the part found within the

12th—15th segments inclusive; (3) that found behind the 15th segment.

In a previous paper[1] I have described at some length the early development of the Wolffian body behind the 16th segment, and I have there shown that that part may be divided into two parts, each characterised by a peculiarity in the early development. In this paper I shall make but little reference to the development of the Wolffian body in this region, confining myself almost entirely to that part lying within the area of the 7th to the 15th segments inclusive.

Development of Wolffian Tubules in region of 7th—11th Segments.

The Wolffian tubules and Wolffian duct in this region attain but a slight development. They may almost be said to have reached their highest point at the stage with fourteen protovertebræ, the only difference in later stages being the development of a lumen in them. The lumen in the tubule may acquire an opening into the Wolffian duct in some cases. In this case the string of cells seen in fig. 5 becomes very short, and the Wolffian duct appears as a narrow groove in the peritoneal epithelium. This state of things is usually found in chicks with from nineteen to thirty-two protovertebræ.

The Wolffian duct in this region exhibits great variations in calibre, and in later stages parts of it appear to atrophy, and isolated portions are found connected with rudimentary tubules. An enlarged section of the Wolffian duct in front is nearly always found as Gasser[2] has described. The duct and tubules in this region appear entirely to atrophy in chicks with more than thirty-five protovertebræ.

I have not thought it worth while to preserve figures of the duct and tubules in this region of the Wolffian body after their first appearance, as the arrangement just described may be easily observed in sections of an embryo chick of the third day.

The interest in the development of this region lies in the fact of the *continuity of development* of the Wolffian tubules and Wolffian duct. It has always appeared to me astonishing that the Wolffian duct developed as a continuous ridge from the intermediate cell mass, which, from our knowledge of Elasmobranch development, may be called the peritoneal epithelium, should entirely separate from it and then secondarily become connected with it by the tubules of the Wolffian body. My investigations, which have been made with some care on a large number of

---

[1] Loc. cit.

[2] Loc. cit.

chicks of all ages from nine to thirty protovertebræ, have entirely convinced me that the usual statements on this point are not true, and show to my mind most conclusively that the duct and tubules of the Wolffian body in the region in question do develop in continuity, precisely as do the duct and peritoneal openings of the head-kidney in most Ichthyopsidan types.

The number of rudimentary tubules in each segment of this region I have not determined precisely. They occur as often as not between the segments, and there seems to be about two for each segment. In the seventh segment I have never seen more than one.

Before proceeding to give an account of the further development in the next region, I will briefly refer to the points in which my observations differ from those of previous observers on the development of the Wolffian duct.

Gasser's account[1] of the development of the Wolffian duct is the most recent and exact. In his valuable paper will be found a complete account of the literature of the subject, to which I need not further refer.

"The first trace of it which he finds is visible in an embryo with eight protovertebræ as a slight projection from the intermediate cell mass towards the epiblast in the region of the three hindermost protovertebræ. In the next stage with eleven protovertebræ, the solid rudiment of the duct extends from the 5th to the 11th protovertebræ; from the 8th to the 11th protovertebræ it lies between the mesoblast and epiblast, and is quite distinct from both, and Dr. Gasser distinctly states that in its growth backwards from the 8th protovertebræ the Wolffian duct never comes into continuity with the adjacent layers. In the region of the 5th protovertebræ, where the duct, &c., was originally continuous with the mesoblast, it has now become free, but is still attached in the region of the 6th to the 8th. In an embryo with fourteen protovertebræ the duct extends from the 4th to the 14th, and is now free between epiblast and mesoblast for its whole extent."

The points in which the preceding account differs from that of Dr. Gasser's briefly are:

1. The position of the continuous ridge of the Wolffian duct.
2. The subsequent complete isolation of the duct in the region of the ridge.
3. The independence of the backward growth of the duct in the 12th to the 15th segment.

I have never seen any trace of the Wolffian duct in front of the 7th segment, and in all the chicks I have examined I find

---

[1] 'Arch. für Mic. Anat.,' vol. xiv.

that the continuous ridge extends from the 7th to the 11th segments.

With regard to Gasser's statement of the complete isolation of the duct in the anterior region from the intermediate cell mass, I can only say that my observations point to an entirely different conclusion.

Thirdly, I differ with him in his statement that the duct in the growth back from the attached extremity does not come into relation with adjacent structures.

As stated above, it seems to me that for the space of four segments the small cord of cells which grows back from the hind end of the ridge, does almost immediately become connected with the intermediate cell mass.

Development of the Wolffian Duct and Body from the 12*th*—15*th Segment.*

I now pass to the most interesting point which has turned up in my investigations on the excretory system of the chick.

In a paper by Mr. Balfour and myself,[1] describing the development of what we believed to be a rudimentary head-kidney in the chick, we drew attention to a structure which so closely resembled the glomerulus[2] of the head-kidney of the Ichthyopsida that we identified it as an homologous structure.

Gasser[3] has also independently discovered and similarly identified this structure.

In the paper just referred to no attempt was made to trace the development of this glomerulus, but it was merely described as it appeared at the time of its greatest development.

The following description is taken from that paper:

"In the chick the glomerulus is paired, and consists of a vascular outgrowth or ridge projecting into the body cavity on each side at the root of the mesentery. It extends from the anterior end of the Wolffian body to the point where the foremost opening of the head-kidney commences. We have found it at a period slightly earlier than that of the first development of the head-kidney....In the interior of this body is seen a stroma with numerous vascular channels and blood-corpuscles, and a vascular connection is apparently becoming established, if it is not so already, between the glomerulus and the aorta. The stalk connecting the glomerulus with the attachment of the

---

[1] 'On the Existence of a Head-Kidney in the Embryo Chick: Studies from the Morphological Laboratory in the University of Cambridge,' Part 1, 1880, and 'Quart. Journ. of Micr. Science,' vol. xix.

[2] I have already given a preliminary account of the development of this structure in the 'Proc. Cambridge Phil. Soc.,' May 3, 1880.

[3] 'Sitzungsberichte der Gesellschaft zur Bedförd d. gesam. Naturwiss.,' No. 5, 1879.

mesentery varies in thickness in different sections, but we believe that the glomerulus is continued unbroken throughout the very considerable region through which it extends. This point is, however, difficult to make sure of, owing to the facility with which the glomerulus breaks away. At the stage we are describing no true Malpighian bodies are present in the part of the Wolffian body on the same level with the anterior end of the glomerulus, but the Wolffian body merely consists of the Wolffian duct. At the level of the posterior part of the glomerulus this is no longer the case, but here a regular series of primary Malpighian bodies is present, and the glomerulus of the head-kidney may frequently be seen in the same section as a Malpighian body. In most sections the two bodies appear quite disconnected, but in those sections in which the glomerulus of the Malpighian body comes into view it is seen to be derived from the same formation as the glomerulus of the head-kidney."

The point which is left in doubt in the above description, viz. as to whether the glomerulus constitutes a continuous structure, is at once decided by a study of its development.

I may here state that it is not a continuous structure, but consists of a series of external glomeruli, each of which corresponds and is continuous with the glomeruli of the Malpighian bodies found in this part of the trunk.

The first development of the Wolffian tubules in the region under consideration has already been described. They appear as outgrowths from the Wolffian duct meeting outgrowths from the intermediate cell mass immediately on the formation of the segment in which they are placed; so that in a chick with fifteen protovertebræ the Wolffian duct is connected with the intermediate cell mass by a certain number of cell cords in the 12th, 13th, 14th, and 15th segments.

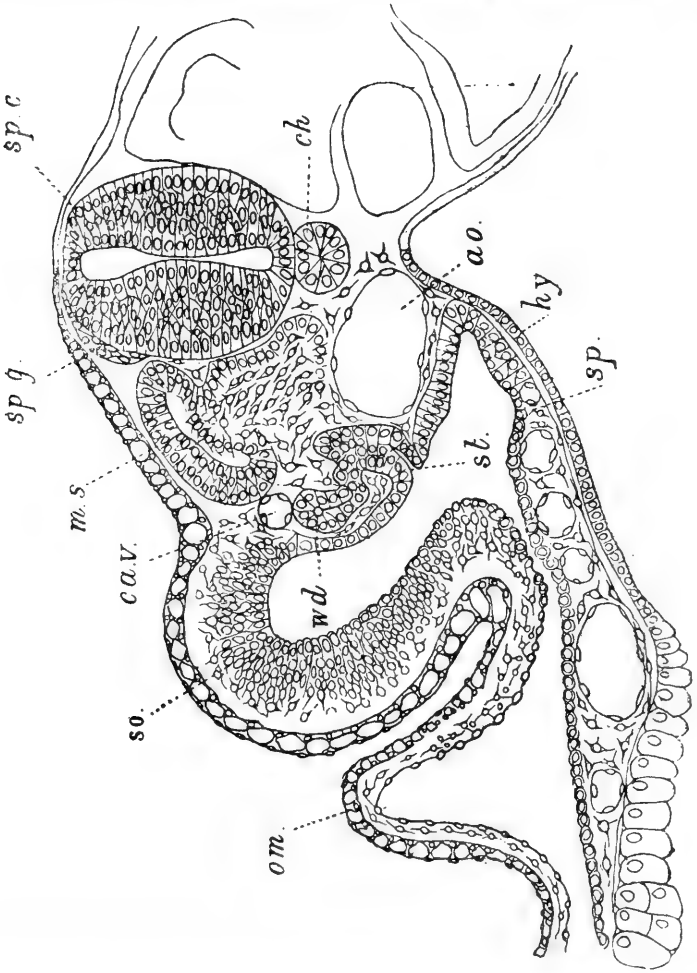
The duct and cords, which have at first rather an irregular outline, soon become well-defined compact structures.

Fig. 12, taken from the 12th segment of an embryo with twenty-two segments, represents the condition of things at this age.

The Wolffian tubules in this region are derived from two distinct structures—(1) the outgrowth from the Wolffian duct; (2) part of the intermediate cell mass.

The intermediate cell mass is at first continuous with the peritoneal epithelium in every section; but, as described in a previous paper, this connection soon becomes lost at certain points (fig. 9), and maintained at others (fig. 10). Figs. 9 and 10 are contiguous sections through the 15th segment of a chick with twenty-two segments, showing this point. At these points, where the continuity is retained, a peritoneal funnel is subsequently formed by the development of a lumen extending from the body cavity into the intermediate cell mass.

The features of the stage of development now reached are well known; it is that of the S-shaped cords of cells which have been so often described. In the adjoining woodcut is represented part of one of these S-shaped strings, showing clearly the above



Transverse Section through the Trunk of a Duck Embryo with about twenty-four Mesoblastic Somites.

am. amnion; *so.* somatopleure; *sp.* splanchnopleure; *wd.* Wolffian duct; *st.* segmental tube; *ca.v.* cardinal vein; *ms.* muscle-plate; *sp.g.* spinal ganglion; *sp.c.* spinal cord; *ch.* notochord; *ao.* aorta; *hy.* hypoblast.

features of a tubule, &c., viz.—(1) the Wolffian duct, in which a lumen has appeared; (2) the outgrowth from it to the intermediate cell mass forming the upper limb of the S; (3) the intermediate cell mass with the commencing lumen from the body cavity.

In the next section the intermediate cell mass is not connected to the peritoneal epithelium.

In chicks of gradually increasing number of protovertebræ this cavity in the intermediate cell mass gradually becomes more marked (figs. 13, 14), and extends into that part of it immediately behind the peritoneal connection (fig. 15).

Figs. 13, 14, and 15 are three successive sections through the 13th segment of a chick with about thirty segments, showing the features of a tubule at this stage.

The Wolffian duct is connected with the lower end of the intermediate cell mass in all the three sections. A distinct lumen has appeared in the intermediate cell mass which opens into the body cavity in front (figs. 13 and 14), but is separate from the body cavity in the hindermost section (fig. 15).

Comparing these figures with figs. 9 and 10 it is seen that fig. 13 or 14 corresponds to fig. 9 in the fact of the continuity between the intermediate cell mass and peritoneal epithelium; while fig. 15 corresponds to fig. 10, in both the continuity having been lost. The difference between them consists in the presence of a distinct lumen in the older series, opening into the body cavity, and continued behind into the part of the intermediate cell mass which has separated from the peritoneal epithelium. This part, marked *i. c. m.* in fig. 15, will in the next stage become converted into that part of the tubule in which a Malpighian body is developed, while the anterior part, which is open to the body cavity, will widen out considerably, and give rise to a wide peritoneal funnel.

In fig. 11 is represented a section through a developing Wolffian tubule in the hinder part of the Wolffian body. The tubule (*w.* t^1.) in this section precisely resembles the part of the tubule (*i. c. m.*) represented in fig. 15. Supposing the anterior part of *w.* t^1. were open to the body cavity it would almost be a repetition of the anterior tubule, save in the fact that it is not yet united to the Wolffian duct. But the hinder tubule (fig. 11) does not develop until after the intermediate cell mass has separated from the peritoneal epithelium, *i. e.* subsequent to the obliteration of the rudiment of the peritoneal funnel.

Not only do the Wolffian tubules in the region of the 12th to 15th segments develop a lumen while still continuous with the peritoneal epithelium, but further, a glomerulus appears in them while still open to the body cavity; and this glomerulus not only appears in the hinder part of the tubule (fig. 15) which has separated from the peritoneal epithelium, but also in the anterior part (figs. 13 and 14) where it is open to the body cavity. This is at once clear on inspection of figs. 16, 17, 18. These figures are taken from the 13th segment of a chick with thirty-four protovertebræ. There was a section not figured between fig. 17 and 18, otherwise the sections are successive, fig. 16 being the anterior.

In fig. 16 is seen the commencement of the peritoneal funnel as a bay lying between the Wolffian duct and mesentery.

In fig. 17, a glomerulus (*gl.*) has appeared projecting into this bay. In the next section, not figured, the bay was almost closed up by an approximation of its edges, while in fig. 18 the bay is completely shut off from the body cavity, and we have a section of a true Malpighian body with its contained glomerulus.

Fig. 18 clearly corresponds to fig. 15 of the previous stage, while fig. 17 corresponds to fig. 14, the difference being that a distinct cellular projection (*gl.*) has appeared at the point where the projection of cells from the Wolffian duct joins the intermediate cell mass.

I have given a diagram (fig. 22) representing an ideal longitudinal dorso-ventral section through two of these Wolffian tubules at this stage. This diagram has been made from a study of many embryos showing the development of the external glomerulus.

The open peritoneal funnel is represented at *p. f.*, the arrow pointing into it. Through it is projecting the anterior part of the glomerulus (*gl.*), that part which I shall call the external glomerulus. A transverse section through this part would give the appearance represented in fig. 17.

Into the closed hinder part of the tubule (*mb.*) is projecting the hinder part of the glomerulus (*i. gl.*), which I shall call the internal glomerulus. It was not possible to represent satisfactorily in this diagram the Wolffian duct, which, obviously from its position in transverse section, would not be seen in a longitudinal section passing through the attachment of the glomerulus.

In fig. 23 is represented somewhat diagrammatically a transverse section through a chick with thirty-three protovertebræ, *i. e.* from a slightly younger embyro than that from which figs. 16—18 were taken, in which the cord of cells connecting the Wolffian duct with the cavity of the glomerulus had acquired a distinct lumen, the cavity of the Wolffian duct being here distinctly continuous with that of the bay in which is placed the rudimentary external glomerulus, and so with the body cavity. At subsequent stages this part of the tubule appears to persist, but only in a rudimentary fashion.

The next stage which I propose to describe was found in a chick in which thirty-six protovertebræ could be counted, but possibly there were more.

The glomerulus has grown immensely (figs. 19, 20, 21), and has now acquired the peculiar histological features which characterise it at the time of its greatest development, and which have already been described in a former paper.

Anteriorly the bay has widened out considerably (fig. 19), and the glomerulus (*e. gl.*) projects directly into the body cavity. Posteriorly the bay remains deep (figs. 20, 21), and the glomerulus almost completely fills it and projects beyond it into the body cavity. In sections behind fig. 21 there was seen a fairly well-developed internal glomerulus.

The edges of the bay are gathering round the glomerulus preparatory to fusing with it, and so closing up the peritoneal funnel and dividing the glomerulus completely into two parts, the internal vascular tissues of which, however, are continuous.

In this stage the epithelial covering of the external glomerulus (*e. gl.*) was distinctly, as in the previous stage, continued behind directly into that covering the posterior internal glomerulus.

When, however, the peritoneal funnel closes by the completion of the process commencing in figs. 20 and 21, this epithelial continuity is lost, and we have the final stage of the glomerulus, the last which I have observed, in which the separation above described is complete, so that in this stage, which is that of the greatest development of the external glomerulus, and corresponds with the commencing formation of the head-kidney, the glomerulus belonging to one tubule is divided into three parts.

(1) An anterior[1] part projecting into the body cavity. This corresponds to a further development of fig. 19.

(2) A middle part, continuous with (1), also projecting freely into the body cavity, but also connected by vascular structures with an internal glomerulus. This part is figured in fig. 26, and corresponds to a further development of the part from which fig. 20 and 21 were taken.

(3) A posterior part, in which there is no external glomerulus, but merely an internal one belonging to a true Malpighian body of the mesonephros, which I have not thought it necessary to figure in this or the previous stage. It is a further development of fig. 18. This stage, which may be observed about the middle of the fourth day of incubation, brings to a close my observations on this extraordinary structure. It appears that in the chick the stage just described is that of the greatest development of the external glomerulus. In the duck, however,

---

[1] Fig. E, Pl. II, in the paper on the 'Head-Kidney of the Chick: Studies from the Morphological Laboratory in the University of Cambridge,' Part 1, 1880, and 'Quart. Journ. Mic. Sci.,' vol. xix.

I have often met with it even larger and more developed, and it appears to me after its separation from the internal glomerulus to get an independent growth, and while the latter is undergoing atrophy to become larger and extend itself posteriorly, so as almost to overlap the external glomerulus of the next tubule.

With regard to the number of the external glomeruli in the chick and the exact limits of their occurrence, the following is briefly what I have been able to make out in a chick with thirty protovertebræ:

In the 11th segment there are two rudimentary tubules running from the Wolffian duct to the peritoneal epithelium. At the point of attachment of these there is a small rudiment of the external glomerulus, visible for only one section in each case.

In the 12th segment there is at the beginning a Wolffian tubule and a well-marked external glomerulus extending through three sections. At the hind end of the 12th segment and beginning of the 13th there is an external glomerulus for three sections continued into part of the segmental tube behind, in which an internal glomerulus will subsequently be developed.

In the 13th segment there is an external glomerulus for three sections.

In the 14th segment there are two segmental tubes with developing external glomeruli.

In the 15th segment no external glomeruli appear to be developed, the segmental tubes being already separated from the peritoneal epithelium.

In later stages only the three or four hindermost of the above external glomeruli appear to develop further. The anterior glomeruli soon atrophy with the adjoining tubules and duct.

In the duck a much greater number become developed, and they may be seen in the anterior segments after their respective tubules have entirely atrophied.

The bearing of the developmental processes above recorded on any hypothesis as to the phylogenetic history of the vertebrate excretory system I propose to examine in the second part of this paper (pp. 41—43; 47).

PART II. *A Discussion of the Vertebrate Excretory System in General.*

The most peculiar feature of the excretory system of the vertebrata is the presence of three more or less distinct parts, the pronephros, the mesonephros, and the metanephros or kidney proper. In the following pages my object will be to explain the relation of these parts, more especially those of the pronephros and mesonephros, and to show that they have arisen as differentiations of a primitively uniform structure.

For this purpose it is necessary briefly to recapitulate the more important features in the development which have a bearing on my argument.

Segmental Duct and Pronephros.

The first part of the excretory system to make its appearance is always a duct. This duct has received various names, but its homology in different forms is undisputed. I shall call it the segmental duct.

In the chick the segmental duct is commonly known as the Wolffian duct.

All the Ichthyopsida whose development is known, with the exception of Elasmobranchs, possess a structure called the head-kidney or pronephros. The pronephros when present always develops in continuity with the anterior end of the segmental duct.

In the Amphibian the segmental duct arises as a groove of the parietal peritoneum, just ventral to the place where the body cavity is connected with the cavities of the muscle plates. This groove, which arises first of all anteriorly just behind the branchial region, is continued for a certain distance backward. It soon, however, becomes constricted into a canal lying between the ectoderm and parietal peritoneum. This constriction has been described as taking place in the following manner:—It first appears in the middle region of the groove, giving rise to a canal opening into the body cavity in front and behind. It then is continued backwards until the groove is completely converted into a canal behind, which soon acquires an opening into the cloaca. Anteriorly the wide opening meanwhile is divided up into two,[1] three,[2] or four[3] openings, according to the species.

The canal immediately behind the last of these openings becomes coiled and placed on the same level but ventral to the openings. The part of the body cavity into which the openings of the segmental duct pass widens out, a vascular projection—the glomerulus—from the dorsal inner wall is formed, extending uninterruptedly from opposite the anterior opening of the segmental duct to as far back as the posterior. The dilated section of the body cavity in which the glomerulus lies, and into which the segmental duct opens, is partially separated from the rest of the body cavity. The whole structure, including openings of duct, ventral coiled part of duct, glomerulus, and dilated part of body cavity, is known as the pronephros. The number of open-

---

[1] Urodela. [2] Anura. [3] Cæcilia.

ings from the segmental duct into the body cavity corresponds with the number of segments through which the pronephros extends.[1]

With its excretory system in this condition the young Amphibian is hatched. Fundamentally the head-kidney retains the above structure, increasing only in size until it begins to atrophy, an occurrence which takes place on the development of the mesonephros.

This method of development of the segmental duct and pronephros is fundamentally repeated in other animals which possess a pronephros.

About the marsipobranch development very little is known. Fürbringer (loc. cit.), quoting W. Müller and his own observations, makes the following statements for Petromyzon:—In the earliest stage which has been observed there was present at about the level of the heart a groove in the parietal peritoneum, which leads behind into a duct, which eventually, by a backward growth, reaches the cloaca and opens into it. The anterior groove or opening of the duct soon becomes divided up into four openings.

In the young Ammocætes there is present a pronephros made up of a complicated coiled duct and four or five openings into the body cavity, opposite which is placed a vascular glomerulus; the whole structure extends over four or five segments.[2] The pronephros atrophies in the adult.

In Myxine nothing is known of the development, but in the adult a pronephros has been described, which, however, is not functional in old individuals (adult ?), as in them it has lost its connection with the backward continuation of the segmental duct.

It[3] consists of the segmental duct, which gives off dorsally a number of diverticula, in which are found glomeruli, and ventrally a number of coiled canals, which open apparently into the pericardial cavity.

The fully-formed pronephros of Petromyzon then resembles in structure very closely that of Amphibia, while the pronephros of Myxine differs in certain important points.

The Teleostei possess a pronephros, which persists as a large organ in the adult. It develops in connection with the seg-

---

[1] Fürbringer, 'Morph. Jahrbuch,' Bd. 3, p. 5.

[2] Scott, in a recent paper ('Morph. Jahrbuch,' vol. viii), states that the segmental duct in Petromyzon, develops as a solid cord of cells from the somatic mesoblast, which subsequently becomes hollow. The peritoneal openings of the head-kidney are developed as outgrowths from the anterior end of this duct to the body cavity.

[3] 'Jenaische Zeitschrift,' vol. vii, 1873.

mental duct precisely as does the pronephros in Amphibia. The only difference between the two is that in Teleostei the segmental duct has never more than one anterior opening, and the part of the body cavity into which it opens, and in which the glomerulus lies, is completely constricted off from the rest of the body cavity, and comes to resemble exactly an enormous Malpighian body.[1]

I may here sum up the common features characterising the ontogeny of the pronephros and its duct (segmental duct) in all the forms of the Ichthyopsida in which the development is at all known:

1. The segmental duct arises first as a ridge from the parietal peritoneum. This ridge usually contains a diverticulum from the body cavity, and is continuously constricted off to form a duct.[2]

2. Except anteriorly, where the constriction only takes place at intervals, leaving the openings of the pronephros (except in Teleostei, where there is only one opening).

3. These openings correspond in number with the segments which the pronephros occupies.[3]

4. A vascular structure, called glomerulus, is formed, projecting on each side of the aorta into a specialised dilatation of the anterior part of the body cavity. Myxine forms a peculiar exception to this otherwise universal fact.

5. This dilated part of the body cavity may become partially or completely separated off to form a capsule, into which the glomerulus projects and the anterior end of the segmental duct opens.

6. The pronephros in all those Ichthyopsida in which it is found attains a functional development, but is usually only active during a period intervening between the hatching and the attainment of full maturity, *i.e.* it only functions in the larva.

In Elasmobranchs, which do not, so far as is known, possess a pronephros, the segmental duct arises as a solid ridge from the somatic layer of the intermediate cell mass in the anterior region of the trunk. From this ridge there grows back a column of cells to the cloaca. On the development of a lumen the segmental duct, with its peritoneal opening, is established. The duct develops quite independently of adjacent structure behind

---

[1] There is a functional head-kidney in adult Ganoids. It appears to be formed on the Teleostean type (vide Balfour, 'Comp., Embryology, vol. 2, p. 51).

[2] In Petromyzon, Scott (see note, p. 445) states that this duct arises as a solid rod of cells, which secondarily becomes connected with the body-cavity epithelium, to form the pronephric funnels. This account, in my opinion, needs confirmation.

[3] 'Fürb.,' p. 5, p. 42.

the point of its original attachment, and does not unite with the segmental tubes till considerably after its first development.

The difference in the development of the segmental duct in the forms possessing a pronephros and in Elasmobranchs is only one of degree.

In both cases it at first arises as a projection, either solid or containing a diverticulum from the body cavity, from the parietal peritoneum just ventral to the muscle plates; but in the one case this groove has a greater longitudinal extension than in the other. In all probability the hinder part of the segmental duct is in all cases formed by an independent growth from the hind end of this groove.

Amongst the Amniota the chick is the type in which the development of the segmental duct has been most carefully examined.

In the chick it arises as in Amphibia as a projection (solid in the chick) from the parietal mesoderm just ventral to the muscle plates; and the extent of the ridge is the space occupied by five segments.

This ridge is constricted off at intervals from the intermediate cell mass, but remains attached at certain points. The hind end of the duct is formed by a growth back from the hind end of this ridge, which takes place independently of adjacent structures.

The question now presents itself: are these structures at the anterior end of the segmental duct in the chick, which so closely resemble in development the openings of the Ichthyopsidan head-kidney, homologous with that head-kidney?

To a consideration of this question I shall return.

Mesonephros.

The mesonephros obtains a large development in all the groups of the Vertebrata; but it does not persist as an excretory organ in the adult of the Amniota.

It develops in three very markedly distinct ways.

The first of these characterises the Elasmobranchii.

The second the Amphibia, Teleostei, Ganoidei, Marsipobranchii.

The third the Amniota.

The Development of Mesonephros in Elasmobranchii.

The segmental tubes of Elasmobranchii were originally described by Balfour as arising as solid diverticula of the peritoneal epithelium. An examination of Balfour's specimens led me, however, to conclude that they originated as specialised parts of the body cavity, viz. from the canals in the intermediate cell mass which connect the muscle plate cavities with the general body cavity; and Balfour has now given his adherence to this view ('Comp. Embryology,' vol. 2, p. 570).

These canals having lost their connection with the body cavity of the muscle plates acquire an opening into the segmental duct, and differentiate[1] into the typical Wolffian tubules. The connection with the general body cavity may or may not be retained in the adult. The secondary tubules develop as outgrowths from that part of the primary tubules, which will give rise to a Malpighian capsule. These outgrowths grow forward and eventually acquire an opening into the terminal portion of the tubule of the segment in front. Later they loose their connection with the Malpighian capsules, though a rudiment of this is sometimes retained as a solid cord of cells.

The method of development of the secondary, tertiary, &c., tubules has not been followed.

The primary tubules open into the segmental duct very shortly after the latter has acquired an opening into the cloaca.

The formation of the Malpighian bodies and the outgrowths from them to form secondary tubules occur later.

For a full account of the development of the mesonephros in Elasmobranchs I must refer to the works of Balfour and Semper, to whom we owe the whole of our knowledge.

Development of the Mesonephros in the remainder of the Ichthyopsida.

As a type of this development I will take an Amphibian, Salamandra, in which animal it has been more completely elucidated by Fürbringer than in any other.[2]

Fürbringer describes the formation of the mesonephros as taking place entirely during larval life; no trace of the gland being seen in the newly hatched larva. It arises as a series of ingrowths of the peritoneal epithelium, which soon become separate from the latter. The primary tubules are hollowed out in the cell masses so formed independently both of the body cavity and segmental duct (Wolffian duct), but subsequently they acquire an opening into both.

The secondary tubules arise in a blastema, the origin of which is not clear, but is apparently derived from the just mentioned serial ingrowths. They acquire an opening into the collecting part of the primary tubule and into the body cavity. The remaining dorsal tubules have an equally obscure origin.

[1] 'Elasmobranch Fishes,' p. 260 *et. seq.*

[2] Loc. cit.

As the mesonephros becomes more developed the pronephros retrogrades, and is eventually entirely, as far as its function is concerned, replaced by the former.

The development of the mesonephros in Teleostei, Marsipobranchii, Ganoidei, is similary described as taking place in the free young (larva) from strings of cells derived from the peritoneal epithelium. In Marsipobranchii as in Amphibia the young are hatched with a functional pronephros, and no trace of the mesonephros; but the former is, in the further growth of the young animal, gradually replaced functionally by the latter, and more or less retrogrades. In the Teleostei, however, and Ganoidei, it persists with the mesonephros as an important functional organ in the adult. In some Teleostei the pronephros is the only functional adult kidney, the mesonephros not being developed.

I have made some observations on the development of the mesonephros in the Frog (*Rana temporaria*), Salmon and Sturgeon, and my observations lead me very strongly to doubt whether Fürbringer and other observers are right in describing the origin of the cells which give rise to the mesonephros as actual ingrowths from the peritoneal epithelium.

In the case of the Frog this is certainly not the case. In fig. 25 is represented a section through a Tadpole of 11 mm., showing the first trace of the cells (K B) from which the Wolffian tubules arise. At their first appearance they are independent of the peritoneum, and only secondarily become connected with it. Fürbringer figures from the Salamander a section in support of his statement; I have also seen such appearances in the Tadpole, but in this animal these strings are only found in that part of the animal in which, I am confidently able to state, no Wolffian tubules are ever developed. I have examined and compared segment with segment of Tadpoles of various ages, and have never found these strings of cells developing into Wolffian tubules. The cell strings appear to me to arise from a blastema of cells developed *in sitû* becoming connected with the peritoneal epithelium, and they are, no doubt, rudimentary tubules.

Fürbringer in his paper gives no evidence of the origin of these cells from the peritoneal epithelium, except a drawing of a stage in which the blastema is connected with the peritoneal epithelium.[1] I have also seen this stage, as mentioned above,

---

[1] Götte also, in his latest writings on the subject, agrees with Fürbringer as to the origin of the cells which give rise to the mesonephros. But I may draw attention to the fact that Götte has held three views on this point, the last of which did not appear (see Fürbringer, loc. cit.) till 1875, *i.e.* after the publication of Balfour and Semper's works on 'Elasmobranchi.'

in my sections of the Frog, but have completely failed to find the earlier stages of this ingrowth. One would expect to see it preceded by a thickening of the very flat cells lining the body cavity at this point; one would hardly expect the flat cells so specialised to form the lining of the body cavity of the young larva suddenly, and without showing any change to begin to grow inward. Further, if the cell cords described by Fürbringer in the Salamander are really only rudimentary structures belonging to the anterior part of the mesonephros, as is certainly the case in the Frog; and if the process which Fürbringer describes for the posterior part of the mesonephros of the Salamander takes place for all fully-developed parts of the mesonephros, as is the case in the Frog, then part of the difficulty caused by the peculiar secondary development of the peritoneal funnels disappears. In other words, I believe Fürbringer has made a mistake, precisely similar to that which was made about the development of the Avian Wolffian body. He has seen in the anterior part of a young larva the cell cords mentioned above; which were present at a time when there was no trace of the posterior part of the mesonephros. He has also seen in the hinder part of older larvæ the blastema of cells separate from the peritoneal epithelium from which the Wolffian tubules arise. Finally, he has connected these two conditions, which are, as I believe, found in different regions of the trunk, and has concluded that the cell strings of the anterior part have separated from the peritoneal epithelium and given rise to the cell masses of the posterior part which really develop independently of the peritoneal epithelium, and eventually give rise to the Wolffian tubules.

My observations on Teleostei lead me, for similar reasons, to assert an origin, *in sitû*, of a continuous blastema, which later, breaking up, will give rise to the Wolffian tubules.

On the other hand, the older observers, including Vogt and Rosenberg for Teleostei, Rathke, Johan. Müller, Reichert, Vogt, for Amphibia,[2] are quoted by Fürbringer as asserting an origin of the tubules as a series of excavations in a blastema of cells lying just internal to the segmental (Wolffian) duct. And it seems to me that the older observers were,[3] as in their statements concerning the development of the mesonephros in the chick, not far from the truth. In the Sturgeon my observations point to a similar conclusion; in the just-hatched young a few mesoblast cells are seen lying internal to the segmental duct. These, at a later stage, are replaced by a more compact mass of

---

[1] 'Fürbringer,' loc. cit., p. 46.

[2] Ibid., loc. cit., p. 12.

[3] Self, 'Quart. Journ. Mic. Sci.,' April, 1880.

cells, occupying the position of which, in a still older animal, Wolffian tubules are seen.[1]

The point I wish to insist upon is that sufficient proof of an actual ingrowth of cell from the peritoneal epithelium has not been given; but that it is much more probable that the kidney blastema arose *in sitû,* in some cases perhaps in continuity with the peritoneal lining, and in other cases independently of it, but soon becoming united with it to form the nephrostomata.

The development of the mesonephros in the Amniota has been most fully elucidated in the chick.[2]

In a recent paper I have described the development of the posterior Wolffian tubules from a continuous blastema of cells derived from the intermediate cell mass; and in the first part of this paper that of the anterior tubules from the cell cords left connecting the Wolffian duct and intermediate cell mass.

Further, in the chick there is a kind of intermediate method of development of the tubules of the 12th—15th segments (see above).

The question here again recurs which was asked before: Are these tubules of the anterior part of the Avian Wolffian body really tubules of the Wolffian body, or have they something to do with the head-kidney? For a discussion of this question I must refer below to p. 460.

The Metanephros.

In a recent paper[3] I have attempted to show that the metanephros, which is found only in the Amniota, is developed from a blastema of cells which arises continuously with but behind the blastema from which the Wolffian tubules develop.

Although the blastema which will give rise to the greater part of the metanephros arises at a comparatively early stage in development, still it is not till a much later stage that it shifts its position, and begins to show signs of developing into the Wolffian tubules. This late development of the kidney, which in this point to a certain extent resembles the Amphibian mesonephros, is a very remarkable fact. I shall return to it again.

I have thus run over very rapidly the most salient features in the development of the various parts of the Vertebrate excretory system, so far as it is at present known to us. I now turn to

---

[1] Balfour has recently described the existence of solid cords of cells, connected with the peritoneal epithelium, in the anterior part of the mesonephros of the sturgeon ('Comp. Embryology,' vol. ii, p. 581). The origin of these cords is not clear, neither is it certain that they undergo full development.

[2] Loc. cit.

[3] Loc. cit.

a consideration of the bearing which these facts have upon any hypothesis as to the phylogenetic connection of these various organs.

But, before so doing, it will be well to consider the nature of the problem which presents itself. It is universally admitted that the Craniata have had a common ancestor. The problem to be solved is contained in these questions: What was the structure and development of the excretory system of that ancestor? How has it been modified to produce the excretory organs which we see in Vertebrates now living?

I am but too well aware how complicated and difficult the problem is, and how insufficient are the data we at present possess to enable us to solve it. Of the two sources (geology and embryology) from which we can hope to obtain these data, palæontology can throw no light whatever upon the primitive Vertebrate or its ancestors, for the Vertebrates have apparently an antiquity greater than that of the oldest fossil-bearing rocks; and even if there are in existence fossiliferous rocks bearing the remains of the ancestor of Vertebrates (excluding Amphioxus), we can hardly hope, when they are found, to obtain any knowledge of the ontogenetic development or structure of soft parts, and the light which palæontology throws upon the later history is at present difficult to use in settling questions of this kind,[1] so that we are thrown almost entirely upon embryology for the facts; but the facts which embryology at present supplies us with are quite inadequate to enable us, even approximately, to solve the problem.

---

[1] In making out the phylogeny of organs which have had an early origin, it seems to me that geology can help us in this way (amongst others). Those forms which are found in the oldest rocks, and which have existed as small isolated groups, very little changed apparently in structure, to the present day, probably retain the same method of development now as then. By examining the embryology of such living forms we might expect to find the development of certain organs different to that in other animals belonging to larger living groups. Turning to the Brachiopoda, a group of great antiquity, we find a development of the body cavity which is shared by but few animals, and which *à priori* we regard as the most primitive method of development of that organ known. Now, of the animals which resemble the Brachiopoda in this respect, Balanoglossus, Amphioxus, and Sagitta are soft bodied, and so not found as fossils; but their very isolation at the present day, with regard to their relations to other groups, suggests that they are survivals of some larger groups, the other members of which have undergone so much evolution that their relationship is unrecognisable. The other group, Echinodermata, which presents this method of development, is found at its greatest development in Palæozoic rocks, and has not undergone any very marked changes since that time. It seems to me that, by following this line, some very important help might be obtained in helping us to decide questions of organ phylogeny.

But still, such as they are, it seems worth while to put them together, and to discuss the conclusions to which they seem to point.

Mr. Balfour[1] has compared the embryonic record to an ancient manuscript in which many leaves are missing, many moved out of their proper order, and many spurious ones interpolated by later hands. It is the duty of an embryologist to try to reconstruct the manuscript and see exactly what it contained when it was first written. In doing this he is aided by the fact that he has access to many copies of the manuscript, which have each been used and altered by very different people. He is thus able, by comparing the different copies, and by studying the characters, &c., of the people by whom they have been possessed, to arrive at a more correct idea as to what the original was like than if he had only one copy.

In studying the various embryonic records we have we can pick out certain features common to all, and which may be assumed to have had their counterpart in the phylogenetic history. But the majority of features have been so altered that it is only possible to arrive at anything like a conclusion by taking into account the complicated conditions in which the animals have lived.

Discussion of the preceding Facts.

While the pronephros is characterised by a very similar structure and development in all the animals in which it occurs, the mesonephros, though possessing in all animals a fairly similar adult structure, presents most remarkable differences in development in the different groups. While the mesonephros is universally (few Teleostei excepted) present, the pronephros is only present in certain forms. Considering first the Ichthyopsida, it is at once seen that the presence or absence of a pronephros is correlated with another peculiarity. When the pronephros is present the egg contains a relatively small amount of food yolk, and the young undergo a considerable part of their development after leaving the egg; while, when the pronephros is absent, the egg contains a very bulky food yolk, and the young undergo far the greater part of their development within the egg (Elasmobranchii).

Further, again considering the Ichthyopsida, we find that one method of development of the mesonephros is found in those animals with a pronephros, while the other method is found in those animals without a pronephros. Of the two methods of development of the mesonephros, while one (that found in

---

[1] 'Comp. Embryology.'

Elasmobranchii) may be considered *as in some respects* primitive, the other must be regarded as very much modified.

Whatever may have been the phylogenetic origin of the Wolffian tubules, the ontogenetic origin, as seen in Amphibia, Teleostei, Ganoids, Marsipobranchii, cannot possibly be regarded as in any way approaching the former. We cannot suppose that a definite serial organ like the mesonephros developed in phylogeny as a series of independent cavities in a mass of mesoblastic cells. At any rate, I think I am justified, in the present state of our knowledge, in making this statement. It is completely opposed to our ideas, and can only be accepted when all other hypothesis as to the origin of the mesonephros in phylogeny, based on the facts of embryology, have been shown to be untenable.

The tubules of the mesonephros in Elasmobranchii, however, in which group they arise from parts of an organ previously developed, present a method of development which is not at all at variance with our *à priori* views as to their phylogenetic origin. From considerations of this kind it seems to me a fair assumption that the development of the tubules in Elasmobranchs from parts of the body cavity more nearly resembles the method by which the organ arose in phylogeny than does that of the Wolffian tubules of the remaining Ichthyopsida.

In Elasmobranchs the Wolffian tubules have a segmental arrangement; one is found in each segment. In all probability this also is a primitive condition.

The arrangement of the tubules in the other vertebrata, although it does not actually afford support to this view, still it does not disprove it. It is a well-known fact that the segmental tubes have very rarely a segmental arrangement in the adult or even in the embryo. But in this connection it must be remembered that the tendency of development always seems to be to render that part of the mesonephros, which is going to function in the adult as an excretory organ, more compact, *i.e.* to bring its constituent parts closer together. I need only refer to the kidneys of the Urodele Amphibia. Here the posterior part of the mesonephros, which is going to function in the adult as kidney, becomes distinguished by its size and the course of its ducts from the anterior part, and in the female by its size only from the anterior part. And Fürbringer has shown, in *Salamandra maculata*, that in correspondence with the increasing size of the posterior region there is found an increased number of primary tubules in a segment, as well as of dorsal secondary tubules.[1]

---

[1] Spengel however asserts, that in the female of those Amphibia he has investigated, the kidney (mesonephros) contains an uniform number of

Spengel has also shown that even in different species of one genus the number of primary tubules in a segment differs, *e.g.* in *Spelerpes variegatus* there is one primary tubule in a segment, in *Spelerpes fuscus* there are two.

Further, Fürbringer states that in the species investigated by him the number of primary tubules in a segment increases with the age of the animal.

"Die Anlagen sind in ihren früheren Entwickelungsstadien leicht zu scheiden; später hingegen lagern sie sich so innig an einander, dass eine Abgrenzung unmöglich wird."[1]

Finally, there seems to be a distinct relation between the closeness of aggregation of the tubules with regard to the body segments and the number of segments found between the mouth and the anus.

In the Anourous Amphibia, where there are very few segments in the adult in this region, we find a very compact and complex kidney.

In the Urodeles, in which the number of segments is greater, the kidney occupies a greater number of segments, and is not nearly so compact, while in Cœcilia, in which the anus is almost terminal, very few segments being placed behind (tail undifferentiated), we find that the kidney is segmental, *i. e.* one primary tubule is found for each segment, and it occupies in the adult as many as sixty segments.[2]

Turning to the Amniota, we find that in Lacertilia[3] the mesonephros has at first a segmental arrangement, one primary tubule for each segment, and although it has not been shown that the fully developed mesonephros of lizards has lost this feature, still there can be little doubt, considering its resemblance to that of Aves, that it has; while in the case of the chick[4] the number of primary tubules in a segment increases with the age of the embryo.

These three facts, viz.—(1) The variability of the number of primary tubules in a segment in closely allied forms, (2) the increased[5] number in a segment as development proceeds, (3) the relation between the compactness of the kidney and the number of segments over which it extends, all point in the same direction. They seem to indicate that the tubules of the Wolffian

---

segmental tubules in each segment over its whole area; while in the male, he finds that they increase in number behind.

[1] Loc. cit., p. 19.

[2] Spengel.

[3] Braun.

[4] Self, 'Quart. Journ. Micr. Sci.,' April, 1880.

[5] There is no evidence that this is effected by intercalation in the chick at any rate.

body are capable of shifting their position according to the wants of the particular species.

We know very well other organs can do this, and I need only mention the anus placed so near the head in frogs, and so far off in Cœcilia, and it seems only probable that an important gland like the kidney should be capable of acquiring a position and arrangement of its constituent parts different from the position of their development, if it is advantageous for the performance of the function of the organ.

The evidence which at the first look appeared so strong against the primitiveness of the Elasmobranch arrangement of one primary tubule to each segment proves on examination to lose a great part of its force.

I now come to a difficulty which apparently at present presents an insuperable obstacle to a successful solution of the question under consideration, viz. What was the structure and development of the excretory system of the ancestral Vertebrate?

Assuming that the development of the Elasmobranch mesonephros presents primitive features in the two details already considered, its development in a third particular can by no means be assumed to be primitive. The fact that the segmental duct develops independently of the tubules cannot, in the present state of our knowledge, be regarded as primitive. Objections of precisely the same kind as those used in arguing against the development of the tubules in Amphibia, &c., being primitive present themselves here.

Any phlyogenetic hypothesis which presents difficulties from a physiological standpoint must be regarded as very provisional indeed. The physiological difficulty present in the conception that in the evolution the mesonephros has arisen by the fusion of two distinct parts, viz. the duct and tubule, is so great that until facts are brought forward to show a different origin we must consent to admit our total ignorance on this point. I think that the observations recorded in the first part of this paper on the development of the Avian Wolffian duct and anterior tubules are of great interest in this relation. Here we have the Wolffian duct and tubules developing in continuity in the anterior part of the excretory system, which has been always admitted to present the most primitive development. But this point I must again keep for later consideration.

So far, then, the following conclusions have been reached—the development of the mesonephros of Elasmobranchii is in part primitive (tubules), and in part very much modified, while the development of the mesonephros of Amphibia, Teleostei, &c., is in all respects modified.

Turning to the development of the segmental duct, we find ourselves obliged, for precisely similar reasons to those already given in the case of the mesonephros, to suppose that that ontogeny is in this respect more primitive in which the duct arises as a continuous groove constricted off from the body cavity than that in which it arises as a solid knob (modified groove) for only a very small part of its course, and undergoing the major part of its early growth quite independently of surrounding structure.

In Elasmobranchii that part which develops as a groove persists as a groove throughout life (abdominal opening of Müllerian duct).

In Amphibia, &c., that part which develops as a groove becomes constricted off first in the middle, and then backwards and forwards, but in front it is constricted in a manner, according to Fürbringer not understood, so as to leave the variable numbers of openings of the pronephros.

However this may be, apparently the openings of the pronephros develop as unclosed portions of the anterior end of the groove from which the duct arose, and they open into a space placed at the root of the mesentery close to the notochord and *close* to the point where in a previous stage the body cavity communicated with the muscle plates.

In the Amphibian, and apparently in the Teleostean, there is no marked structure corresponding to the intermediate cell mass of Elasmobranchii. The muscle-plate cavity is, after its separation from the general body cavity, only separated from the latter by a double layer of cells, forming its ventral wall and the wall of the body cavity; *i. e.* there is no portion of the body cavity at first continuous, but subsequently divided up by the coming together of its walls into a series of canals connecting the general body cavity with the muscle plates.

Now the glomerulus of the pronephros develops in a part of the body cavity anatomically corresponding to the intermediate cell mass of Elasmobranchii, only in Amphibia it does not, in this region, become divided up into chambers corresponding to the segments.

With this part of the body cavity, from the somatic walls of which the original groove arose, the openings of the head-kidney communicate. The number of these openings corresponds with the number of segments occupied by the pronephros in all those animals in which they exceed one, except Myxine; but the development of the pronephros in Myxine is not at all known, and its adult structure is, on the whole, obscure.

Turning again to Elasmobranchs, we find that the anterior knob of the segmental duct arises from the intermediate cell mass, *i. e.* from a part of the body cavity corresponding serially with that with which in the succeeding segments it later unites when the young segmental tubes acquire a communication with the segmental duct.

In Amphibia the segmental duct, when larval life is tolerably advanced, opens into a Wolffian tubule, which arises from a mass of cells, the origin of which is obscure, but which apparently does not appear till after the larva has left the egg. Now the Wolffian tubule of an Amphibian is homologous with that of an Elasmobranch; it is similarly constructed, and opens into the body cavity at a corresponding point. Hence we are driven to the conclusion that the cells from which the Wolffian tubule in an Amphibian arise are homologous with the intermediate cell mass of an Elasmobranch.

But in Amphibia these cells are not developed where, if Elasmobranch development is primitive, they should be; and appear later in a way which gives no clue to their relationship to the intermediate cell mass in Elasmobranchii.

What is the meaning of this extraordinary method of development?

In Elasmobranchs the development of the segmental duct is modified, while the development of the mesonephros is primitive in its segmental arrangement and origin as a specialised part of an organ present at an earlier stage.

In Amphibia the development of the segmental duct is more primitive, but that of the mesonephros very modified, and this very latter fact always goes hand in hand with the presence of a pronephros. Turning to the pronephros, it is found to develop *in continuity* with the segmental duct. It is found to possess, with regard to its openings into the body cavity, a segmented structure. It is also found to possess a structure, the glomerulus, resembling extraordinarily closely the glomerulus of an ordinary Malpighian body of the mesonephros. This glomerulus lies in a special part of the body cavity, just as a glomerulus of a Malpighian body in the mesonephros of an Elasmobranch lies in what from its origin may be called a specialised part of the body cavity; and both these specialised sections in their anatomical position precisely correspond (see above, p. 38).

With all these similarities can the inference be avoided that the head-kidney is descended from the same primitive excretory system as the mesonephros, which has appeared early in development to supply the larva with an excretory organ, and has been able to retain a more primitive development? The larva, having this, has not wanted the hinder part, and in consequence, having all its energy occupied while within the egg in developing those organs which it will really require as a larva, it leaves over the development of the organs not so required until after it is hatched; and in order that it may not be burdened by useless organs, the cells from which the tubules after appear and which should appear, if keeping the phylogenetic order, quite early in embryonic life, in a way already indicated, are reduced so as hitherto to have escaped observation.

It is perfectly true that the pronephros does present peculiarities of structure not presented by the mesonephros, such as the unsegmented nature of the glomerulus, and in the fact that the tube connecting the cavity in which the glomerulus lies with the segmental duct not being coiled. But in the fundamental structure, *i.e.* in the possession of a glomerulus placed close to the main vascular channel (aorta), in the segmental arrangement of the openings of the segmental duct into the cavity (anatomically corresponding in both cases) containing the glomerulus, in the cavity containing the glomerulus being a specialised part of the body cavity; in all these points the pronephros and mesonephros resemble each other.

Assuming for the moment the truth of this suggestion, we find the pronephros to present that method of development which *à priori* we are bound to assume would be if it were not for disturbing causes, the development of the mesonephros, because it represents the most probable method by which the mesonephros and its duct can have arisen in phylogeny.

The question now arises, What are the disturbing causes which in Amphibia have so changed the phylogenetic development? The answer has already been given, but I will repeat it here. It has been brought about by the action of natural selection on the innumerable larvæ produced, so that only those animals reached the adult state which in their prelarval and larval development conformed to the type of development we have before us.

Admitting the possibility of both prelarval as well as larval development varying at any particular stage, the tendency has been to produce a dissimilarity in the early structure of the excretory organs of Elasmobranchii and Amphibia greater than that which exists in the adult state, a result entirely in opposition to what we should expect from the application of that principle which has been laid down as regulating embryonic development, viz. that embryos of different animals, starting as fairly similar, become more and more dissimilar as their development proceeds.

To get any actual proof from embryonic development in favour of the above hypothesis must, from the nature of the case, be very difficult. For the very reason of the existence of the pronephros as an anterior part of the excretory system well marked off from the posterior makes it improbable that anything more than a trace of the hinder part should appear simultaneously in embryonic development with the anterior part. If the rest of the mesonephros developed continuously with the duct and simultaneously with the pronephros, then, on the above hypothesis, we should not be able to distinguish a pronephros from the hinder part; and it is opposed to all our ideas of economy to suppose that a rudiment of the mesonephros should appear at what phylogenetically would be the proper time, remaining over as a rudiment in the larva, *i. e.* as a useless organ forming merely a burden until it was wanted.

It seems to me that we can only expect, at the very utmost, to find a very small trace of the mesonephros in embryonic development at what phylogenetically we should consider, on the above hypothesis, to be the proper moment relative to the pronephros.

I have been examining the development of the segmental duct in an Amphibian, the frog, to see if at the time of closure of the groove of the segmental duct any trace of a discontinuous closure such as we find in the head-kidney existed. If the pronephros is merely the anterior part of a segmental organ of which the mesonephros is the posterior part, and if phylogeny is in any way repeated in the development of the pronephros, we should expect to find that the discontinuous (segmented, see above) closure of the pronephros would be repeated behind, showing some traces at least of the openings of the segmental duct and of the specialised part of the body cavity which later forms the Wolffian tubule and contains the glomerulus. So far it cannot be said that my search has been from my point of view successful. To get any evidence of what I was searching for requires a very complete series of sections in a state of preservation favorable for observation. The difficulties presented by the embryonic Amphibia in their early stages to such a successful result are very great. In the first place they are very brittle, and comparatively very few of the sections, even if thick, can be mounted uninjured. Of these, very few, indeed, can be obtained perfect, and those so obtained are apparently more difficult to see anything in than the thick ones. The cells are full of yolk granules which seem to escape and obliterate the outlines of the cells from the sight.

While my results have not been such as to unable me to speak with any confidence either one way or the other, yet on the whole they have convinced me that a re-examination with a new method of the development of the segmental duct in Amphibia, &c., would repay the trouble.

In the chick, on the other hand, the anterior part of the segmental duct, for the space of five segments, develops exactly in the manner of the segmental duct and head-kidney of the Ichthyopsida. Are the cell cords connecting the duct and peritoneal epithelium in these segments rudimentary Wolffian tubules, or are they rudiments of a head-kidney? In the absence of a continuous glomerulus opposite them they differ from the openings of the pronephros. In their development they resemble the latter. If they are Wolffian tubules they develop quite differently from all other Wolffian tubules. If they are rudimentary pronephric funnels, then the chick possesses a rudiment of a pronephros which resembles exactly the hinder developing Wolffian tubules.

It seems to me that these structures, under the light of the above hypothesis, present no difficulty, and I cannot help thinking that the discovery of their method of development is striking evidence in its favour. They belong, on that hypothesis, to the anterior part of the excretory organ, which has retained the primitive method of development originally characterising the whole organ. They, in some Avian ancestor, have constituted the first developed part of the excretory system, which has been utilised by the larva as its excretory organ. Supposing that Avian ancestor existed now, we should find that its larva possessed an organ which we should call pronephros, having a structure less modified probably from the hinder part of the excretory system than in the case of the Ichthyopsida, *i.e.* an organ the serial homology of which, with the mesonephros, would no more be disputed than is that of the metanephros with the mesonephros.

It may be objected to this view of the anterior part of the Avian excretory system, that it differs in certain marked features from the pronephros of other forms. Of these differences the most important is, perhaps, the fact that there is always found an interval unoccupied by segmental tubes between it and the mesonephros. But in Amphibia Salamandra Fürbringer[1] distinctly states that rudiments, as masses of cells, occupying the same relative position to the segmental duct as do segmental tubes, are found intervening between the two. If these rudimentary tubules underwent full development there would be no such gap as that we now find between the pro- and mesonephros of Amphibia.

But this difficulty is merely part of another difficulty which it seems to me must exist whatever view be taken of the nature of the pronephros, namely, why does this organ, so well developed in the larva and apparently perfectly well performing the functions of an excretory organ, atrophy in the adult? And this difficulty only seems capable of the unsatisfactory explanation,

---

[1] Loc. cit.

that though perfectly well suiting the requirements of the larva, its position is unsuitable for the satisfactory performance of its functions in the adult. Balfour has suggested[1] that the atrophy of the pronephros is due to its position in that part of the body cavity which eventually becomes the pericardium; and has pointed out, as a confirmation of this view, that it only persists in the adult of those animals in which it is completely shut off from the body cavity, *e.g.* Teleostei.

(The enormous size which the pronephros attains in adult Teleostei is peculiar, but, coupled with the remarkably feebly developed mesonephros in the adult, is not astonishing. The pronephros seems capable of carrying on all the excretory work in some adult Teleostei, in which the mesonephros is not present. The absence of the mesonephros in these cases is probably purely secondary, and, no doubt, traces of it would be found if a close examination were made. The survival of a larval character into the adult state is paralleled by the Axolotl's gills.)

A second feature of difference between this anterior part of the Avian excretory system and the Amphibian pronephros, is the absence in the former of a continuous glomerulus. This may be abortion from disuse, and does not really present a serious difficulty.

A third feature of difference is that the Avian pronephros extends over a much greater area than that of the Ichthyopsida, but when I draw attention to the fact that this difference is found amongst the various members of the Ichthyopsida themselves, I think it can hardly be looked upon as a difficulty. In Teleostei the head-kidney is distinguished by one peritoneal opening and a correspondingly short glomerulus. From this we have all stages to the five peritoneal openings of Petromyzon.

Finally, even if the Avian pronephros did differ in certain features from the Ichthyopsidan pronephros, this can hardly be regarded as a serious difficulty.

The pronephros of Teleostei with its Malpighian capsule containing the isolated glomerulus, and with its one peritoneal opening, surely differs considerably from the pronephros of the frog with its three peritoneal openings and its glomerulus lying free in the body cavity.

Again, without laying too much stress upon it, I point to the pronephros of Myxine, which differs still more remarkably from that of other types.

The difficulty presented by the Elasmobranchii, in which the tubules, though retaining certain primitive features of development, do not develop in continuity with the duct, is very great,

---

[1] 'Comp. Embryology,' vol. ii.

and in the present state of our knowledge no satisfactory explanation, founded on facts of development, can be given of it. I will suggest a possible, but entirely rough and hypothetical, solution on the lines so far followed.

Before the Elasmobranchii produced eggs with the large food yolk they at present possess, they may have undergone a large part of their development in the surrounding medium as free larvæ. These larvæ must have left the egg at a time when the cavities of the muscle plates were still open to the body cavity, and when the segmental duct had only just commenced to be formed in front, and before the development of the vascular system, and therefore before the glomerulus, the functions of which were probably carried on by the walls of the body cavity. The segmental duct was quickly developed from a groove into a duct, the larvæ thus precociously developing a recently acquired adult structure. With this constitution the larva of the ancestral Elasmobranch quickly developed the rest of its excretory system. In consequence of the larva having been hatched at a very primitive stage, before the muscle plates were separated from the body cavity, certain primitive characters in the development of the segmental tubes were retained. These characters have been more or less transmitted to the present day, this having been rendered possible by the acquisition of food yolk and abolition of the larval state.

However this may be, and it is useless now to make hypotheses of this kind, we can only wait till a more close study of Elasmobranch development has been made to see if any traces can be found of the disturbing cause which has produced the modification in the development of the excretory system assumed on the above hypothesis, and very possibly in the search along the lines which this hypothesis indicates quite a different view as to the phylogeny of the vertebrate excretory system may present itself.

Before concluding I will briefly state what I think to have been the structure of the primitive excretory system in the ancestral Vertebrate.

There was a duct occupying the position of the segmental duct, *i. e.* at the dorsal outer angle of the body cavity, at the point where the latter becomes separated from the cavities of the muscle plates. This duct opened in each segment into the dorsal part of the body cavity. On the inner wall of the latter projected on each side a vascular ridge formed by the aorta. Behind, the segmental duct opened into the cloaca.

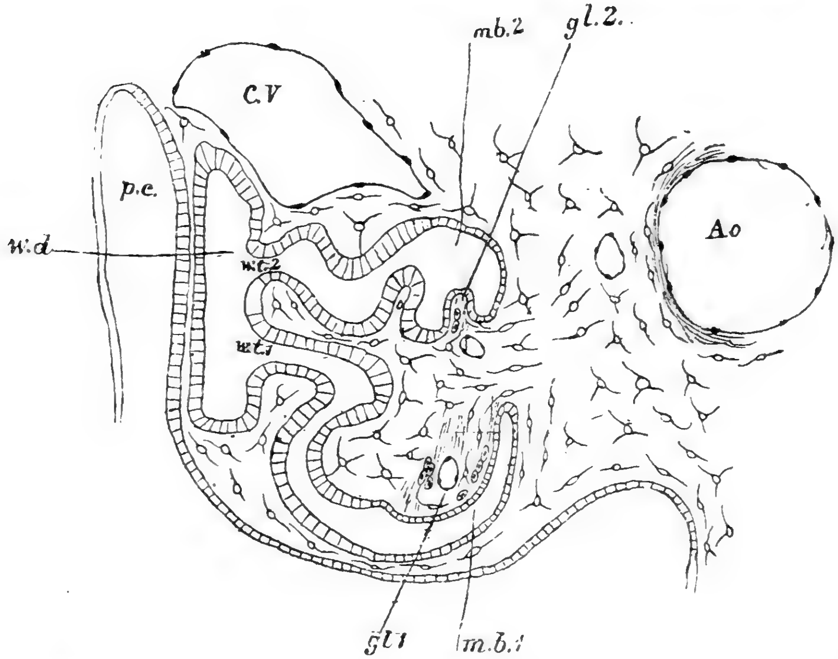
As differentiation proceeded the vascular aortic ridge became more especially developed opposite each opening of the segmental duct, and parts of each of these enlargements became successively enclosed in a special part of the body cavity, giving rise to the commencement of the secondary glomeruli. With this division of the glomerulus segmentally, and of each segment of it into further secondary glomeruli, each lying in a specialised part of the body cavity, the openings of the segmental duct began to fold and divide, incompletely at first, into special openings, one for each secondary glomerulus. Finally, this division was completed, and the segmental duct communicated by a number of openings in each segment with specialised parts of the body cavity containing a portion of the original aortic ridge. The specialised parts containing these glomeruli being still open to the body cavity, and the glomeruli being still all distinctly attached by a common stalk to the walls of the body cavity, and the intermediate parts of the original continuous ridge having completely vanished, now the capsules enclosing the glomeruli became more and more completely marked off from the body cavity. The openings putting them in communication with the segmental duct elongated into tubules which became coiled, and the glomeruli themselves gained a greater independence of each other by a development of intermediate tissue.

A trace of the original state of things has descended to the present time in the pronephros, with its continuous glomerulus opposite the opening of the segmental duct, and placed in a specialised part of the body cavity. Differences in structure from the supposed primitive state of things have of course arisen, in consequence of the specialisation of the pronephros as the larval excretory organ.

In the same way a trace of the division of the primary glomeruli into primary, secondary, &c., glomeruli, is left in the curious development of the external glomeruli of the anterior part of the Avian mesonephros. Only in this case no cause can apparently be given for the retention of this primitive feature of development.

An examination of an early stage in the development of the Avian Wolffian tubules, when the primary and secondary tubules are both fairly well established, but not very complicated in structure, points very distinctly to the fact that the glomeruli of the two tubules are parts of one primitive glomerulus. They appear to be continuous, and while one looks ventrally, *i. e.* the so-called primary glomerulus, the other looks dorsally. A glance at the accompanying woodcut will make this clear.

If this drawing of a section through the Wolffian body of a chick in a part with primary and secondary tubules, be compared with fig. 24, which is from the anterior part of the same chick where there are no secondary tubules, it will be seen that the step between them is not great.[1] It is merely necessary to suppose the division of the glomerulus (in fig. 24) into two parts, and a simultaneous development of certain folds from the Wolffian duct to form the tubules, and the original single tubule would have been transformed into a ventral primary and a dorsal secondary tubule.



Further, as I have pointed out in another paper,[2] the secondary tubule always arises in close proximity, apparently from a blastema continuous with a part of that from which the primary tubule arose.

A modification of development is to be expected, because in those animals in which the mesonephros develops after hatching, it clearly comes gradually into use. The whole is not wanted at once, but with the increasing size of the larva, more tubules are wanted. The first developed (primary) in Salamandra acquire a structure with which they can apparently perform their function when there is hardly a trace of the secondary tubules (Fürbringer, loc. cit., fig. 26).

---

[1] It will be observed that in this figure the tubule connecting the Wolffian duct and capsule is hardly developed. In all probability, this was on the analogy of the pronephros, the primitive state of things, the tubule, being a secondary differention of the duct near each glomerulus.

[2] 'Quart. Journ. Micr. Sci.,' April, 1880.

A cause of abbreviation is so clear in this case that I need not waste time in stating it.

But the whole details of the development of the secondary, &c., dorsal tubules needs reworking, for, with the exception of the observation of Mr. Balfour's for Elasmobranchs, we have no real knowledge of their exact method of development. The result of such an investigation cannot but be exceedingly interesting from a phylogenetic standpoint.

I cannot help thinking, as before stated, that the development of the external glomeruli in the chick may have some interest in this relation.

The modification of the mesonephros of the Amniota is, on the above hypothesis, due to the fact that some Avian ancestor possessed a larva in which the anterior part of the excretory system was early developed, the development of the hinder part being deferred, and consequently modified, just as we see to be the case now in the Ichthyopsida.

The still greater modification und retardation of the development of the metanephros or true kidney of the Amniota, and the great size which the Wolffian body reaches in the embryo, are striking facts which demand consideration in any discussion of the Vertebrate excretory system.

In my paper on the "Development of the Kidney" I have stated my views on the relation of the Amniote kidney to the mesonephros. But one point in that paper is left untouched.

Why does the kidney appear so late? and also why does the Wolffian body become so large and complex—so much larger than the small-sized chicks, in which it is fully developed, can need?

And, further, why should this organ, apparently so well adapted to serve as the excretory organ of the adult chick, atrophy?

It may be said, in answer to the latter question, that only those tubules of the mesonephros which open into the cloaca independently of the Wolffian duct can function in the adult, as those which have not so changed their course would interfere with the function which the Wolffian duct later acquires—the carriage of semen.

It seems to me that the only answer which can be given to the first of these questions is this:

The kidney is thrown back in development for the same reason that the mesonephros of the Amphibia is, viz. because the ancestor of the chick underwent part of its development out of the egg, at which stage of development the testis, not being developed, did not interfere with the excretory functions of the Wolffian tubules, or *vice versâ*. The large size of the mesonephros, then, is to be explained on the supposition that the larva of the chick's ancestor used it for a considerable period of its early life as an excretory organ, so that it may be said that the pronephros holds the same general relation to the mesonephros in the Ichthyopsida as does the mesonephros to the metanephros in the Amniota.

I do not mean to affirm that the above explanation of the lateness of the development of the metanephros is absolutely valid, for I think that a careful consideration of the development of the hind part of the mesonephros in Amphibia and Elasmobranchii might necessitate a slightly different explanation.

But an explanation of that kind must be sought to explain the remarkably late development in the chick of an organ which phylogenetically must be assumed to have had an origin simultaneous with that of the mesonephros.

With regard to the relation which the testes enters into with the mesonephros, it is interesting to notice the modified development which always characterises this connection.

Here it can be definitely affirmed that the lateness and consequent modification of the process is due to the fact that the apparatus has not been required in the larvæ of the Ichthyopsida and of the Amniote ancestors, and consequently has been put off and modified in development. The explanation is exactly similar to that given for the modification in development of the Amphibian mesonephros, except that here we are supposed to be able to assert with greater reason that the putting off and consequent modification is due to the fact that the connection between the testes and mesonephros was not wanted sooner, and so was not developed.

Summary of the Hypothesis and main Arguments used.

The whole of the Vertebrate excretory system, including pronephros, mesonephros, and metanephros, are derived from a primitive organ possessed by the ancestral Vertebrate. This organ had a segmental character, and consisted of a duct, the segmental duct opening in every segment into the body cavity, close to a continuous structure, known now as the glomerulus, which was placed close to the main vascular channels and acted as an excretory organ.

The anterior end of this organ was used by the larva, and developing more or less with regard to other structures at the normal time, retained many primitive features of development originally characterising the whole organ, and is known to us as the pronephros. The posterior part of the organ had its development delayed with regard to other structures, particularly those in connection with which it primitively developed; the development was consequently modified. This part is known to us as the mesonephros.

The same hypothesis was applied to account for the retardation and modification of the development of the metanephros with regard to the mesonephros in the Amniota.

The main facts in favour of the hypothesis are—

1. The development of the segmental tubes in Elasmobranchii and of the pronephros and segmental duct of the Ichthyopsida as parts of the body cavity.

2. The obvious modification in development of the mesonephros, accompanying also the presence of a pronephros in most of the Ichthyopsida.

3. The resemblance in structure between the pronephros and mesonephros, particular stress being laid on the fact that *the glomerulus in both glands is developed in anatomically corresponding,* i. e. *homologous, parts of the body cavity*

I may point out before leaving the subject that other views concerning the nature of the pronephros have been expressed by Gegenbaur, Fürbringer,[1] and Balfour.[2] The two former authors look upon the pronephros as having an antiquity greater than that of Vertebrates, greater even than that of the segmented ancestors of Vertebrates. They regard it as being descended from the primitive excretory system possessed by the unsegmented ancestor, which has been retained in such forms as Turbellaria and Rotifera, the segmented posterior part having been added when the segmented state was reached.

Müllerian Duct.

Balfour's views as to the phylogeny of the Müllerian duct and its homology throughout the Vertebrata are well known. He supposes it is one or, in the chick, more of the head-kidney openings which have become modified for generative purposes.

I still adhere to the view expressed in the paper on the "Rudimentary Head-Kidney of the Chick" as to the meaning of the peculiar structures at the anterior end of the Müllerian duct, and I think that there are grounds, which it is not necessary to enter into here, for supposing that the abdominal opening or openings of the Müllerian duct have been derived from the anterior part of the excretory system after its modification to form the pronephros. But I quite admit that a fuller knowledge of the early development of the Elasmobranch segmental duct may necessitate an alteration in this view.

---

[1] Loc. cit.

[2] Balfour looks upon it as the most primitive part of the excretory system which has been retained by the larva, as so many ancestral organs are, long after they have been lost by the adult. 'Comparative Embryology,' vol. ii.

DESCRIPTION OF PLATES IV AND V.

PLATE IV.

Fig. 1.—Transverse section through the pelvic fin of an embryo of *Scyllium* belonging to stage P,[1] magnified 50 diameters. *bp*, basipterygium; *br*, fin-ray; *m.* muscle; *hf*, horny fibres supporting the peripheral part of the fin.

Fig. 2.—Pelvic fin of a very young female embryo of *Scyllium stellare*, magnified 16 diameters. *bp*, basipterygium; *pu*, pubic process of pelvic girdle (cut across below); *il*, iliac process of pelvic girdle; *fo*, foramen.

Fig. 3.—Pelvic fin of a young male embryo of *Scyllium stellare*, magnified 16 diameters. *bp*, basipterygium; *mo*, process of basipterygium continued into clasper; *il*, iliac process of pelvic girdle; *pu*, pubic section of pelvic girdle.

Fig. 4.—Transverse section through the ventral part of the trunk of an embryo *Scyllium* of stage P, in the region of the pectoral fins, to show how the fins are attached to the body, magnified 18 diameters. *br*, cartilaginous fin-ray; *bp*, basipterygium; *m*, muscle of fin; *mp*, muscle-plate.

Fig. 5.—Transverse section through the ventral part of the trunk of an embryo *Scyllium* of stage P, in the region of the pelvic fin, on the same scale as fig. 4. *bp*, basipterygium; *br*, cartilaginous fin-rays; *m*, muscle of the fins; *mp*, muscle-plate.

PLATE V.

Fig. 6.—Pectoral fin of an embryo of *Scyllium canicula*, of a stage between O and P, in longitudinal and horizontal section (the skeleton of the fin was still in the condition of embryonic cartilage), magnified 36 diameters. *bp*, basipterygium (eventual metapterygium); *fr*, cartilaginous fin-rays; *pg*, pectoral girdle in transverse section; *fo*, foramen in pectoral girdle; *pe*, epithelium of peritoneal cavity.

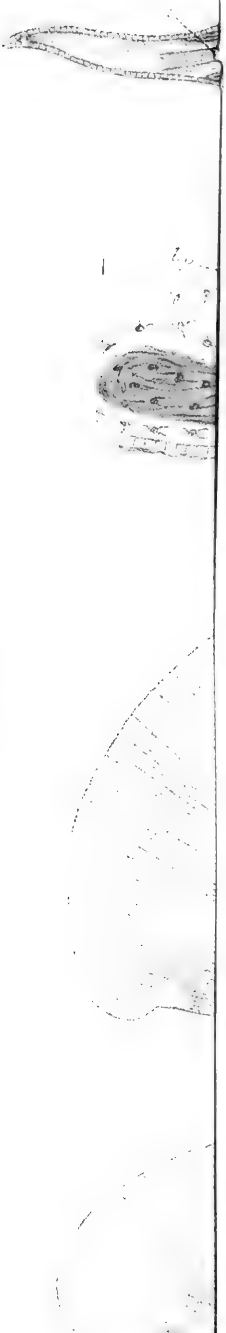
Fig. 7.—Transverse section through the pectoral fin of a *Scyllium* embryo of stage P, magnified 50 diameters. *bp*, basipterygium; *br*, cartilaginous fin-ray; *m*, muscle; *hf*, horny fibres.

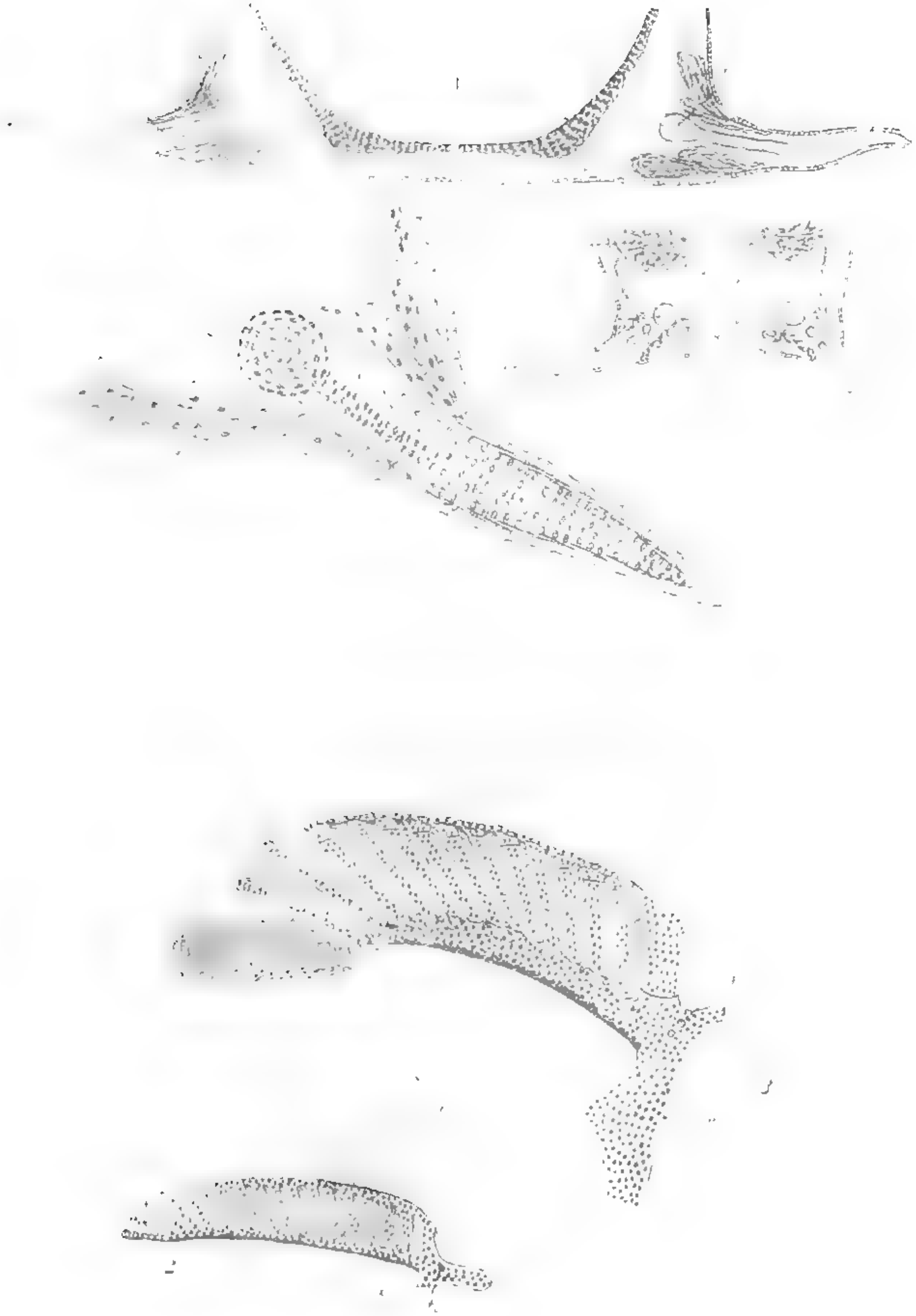
Fig. 8.—Pectoral fin of an embryo of *Scyllium stellare*, magnified 16 diameters. *mp*, metapterygium (basipterygium of earlier stage); *me.p*, rudiment of future pro- and mesopterygium; *sc*, cut surface of a scapular process; *cr*, coracoid process; *fo*, foramen; *hf*, horny fibres.

Fig. 9.—Skeleton of the pectoral fin and part of pectoral girdle of a nearly ripe embryo of *Scyllium stellare*, magnified 10 diameters. *mp*, metapterygium; *mes*, mesopterygium; *pp*, propterygium; *cr*, coracoid process.

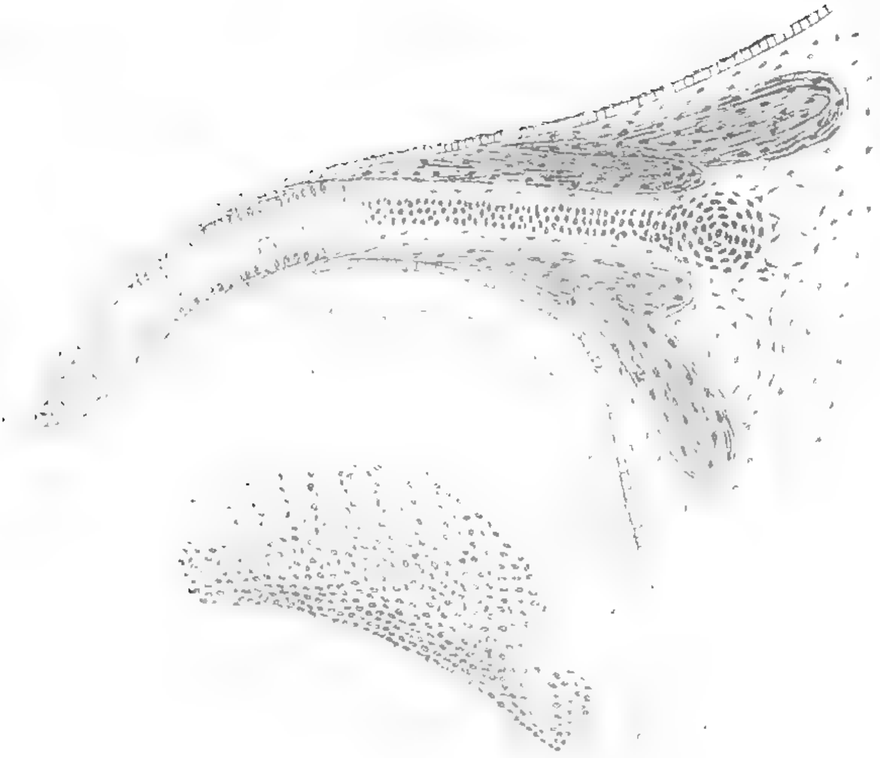
---

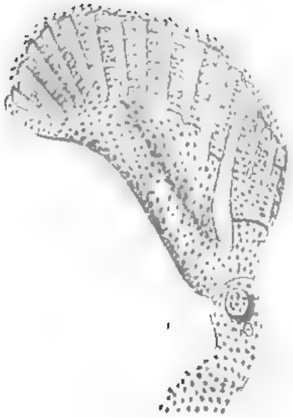
[1] I employ here the same letters to indicate the stages as in my Monograph on Elasmobranch Fishes.





FINS OF ELASMOBRANCHS





On the DEVELOPMENT *of the* SKELETON *of the* PAIRED FINS *of* ELASMOBRANCHII, *considered in relation to its bearings on the* NATURE *of the* LIMBS *of the* VERTEBRATA.

By F. M. BALFOUR, F.R.S., F.Z.S., Fellow of Trinity College, Cambridge.

(With Plates IV and V.)

SOME years ago the study of the development of the soft parts of the fins in several Elasmobranch types, more especially in *Torpedo,* led me to the conclusion that the vertebrate limbs were remnants of two continuous lateral fins.[1] More or less similar views (which I was not at that time acquainted with) had been previously held by Maclise, Humphry, and other anatomists; these views had not, however, met with much acceptance, and diverge in very important points from those put forward by me. Shortly after the appearance of my paper J. Thacher published two interesting memoirs comparing the skeletal parts of the paired and unpaired fins.[2]

In these memoirs Thacher arrives at conclusions as to the nature of the fins in the main similar to mine, but on entirely independent grounds. He attempts to show that the structure of the skeleton of paired fins is essentially the same as that of the unpaired fins, and in this comparison lays special stress on the very simple skeleton of the pelvic fin in the cartilaginous Ganoids, more especially in *Acipenser* and *Polyodon.* He points out that the skeleton of the pelvic fin of *Polyodon* consists essentially of a series of nearly isolated rays, which have a strikingly similar arrangement to that of

---

[1] 'Monograph on the Development of Elasmobranch Fishes,' pp. 101, 102.

[2] J. K. Thacher, "Median and Paired Fins; a Contribution to the History of the Vertebrate Limbs," 'Trans. of the Connecticut Acad.,' vol. iii, 1877.

J. K. Thacher, "Ventral Fins of Ganoids," 'Trans. of the Connecticut Acad.,' vol. iv, 1877.

the rays of the skeletons in many unpaired fins. He sums up his views in the following way:[1]

"As the dorsal and anal fins were specialisations of the median folds of *Amphioxus*, so the paired fins were specialisations of the two lateral folds which are supplementary to the median in completing the circuit of the body. These lateral folds, then, are the homologues of Wolffian ridges in embryos of higher forms. Here, as in the median fins, there were formed chondroid and finally cartilaginous rods. These became at least twice segmented. The orad ones, with more or less concrescence proximally, were prolonged inwards. The cartilages spreading met in the middle line; and a later extension of the cartilages dorsad completed the limb-girdle.

"The limbs of the Protognathostomi consisted of a series of parallel articulated cartilaginous rays. They may have coalesced somewhat proximally and orad. In the ventral pair they had extended themselves mesiad until they had nearly or quite met and formed the hip-girdle; they had not here extended themselves dorsad. In the pectoral limb the same state of things prevailed, but was carried a step further, namely, by the dorsal extension of the cartilage constituting the scapular portion, thus more nearly forming a ring or girdle."

The most important point in Thacher's theories which I cannot accept is the derivation of the folds, of which the paired fins of the Vertebrata are supposed to be specialisations, from the lateral folds of *Amphioxus;* and Thacher himself recognises that this part of his theory stands on quite a different footing to the remainder.

Not long after the publication of Thacher's paper, an important memoir was published by Mivart in the 'Transactions' of the Zoological Society.[2] The object of the researches recorded in this paper was, as Mivart explains, to test how far the hard parts of the limbs and of the azygos fins may have arisen through centripetal chondrifications or calcifications, and so be genetically exoskeletal.[3]

Mivart's investigations and the majority of his views were independent of Thacher's memoir; but he acknowledges that he has derived from Thacher the view that pelvic and pec-

---

[1] Loc. cit., p. 298.

[2] St. George Mivart, "On the Fins of Elasmobranchii," 'Zoological Trans.,' vol. x.

[3] Mivart used the term exoskeletal in an unusual and (as it appears to me) inconvenient manner. The term is usually applied to dermal skeletal structures; but the skeleton of the limbs, with which we are here concerned, is undoubtedly not of this nature.

toral girdles, as well as the skeleton of the limbs, may have arisen independently of the axial skeleton.

The descriptive part of Mivart's paper contains an account of the structure of a great variety of interesting and undescribed types of paired and unpaired fins, mainly of Elasmobranchii. The following is the summary given by Mivart of the conclusions at which he has arrived :[1]

"1. Two continuous lateral longitudinal folds were developed similar to dorsal and ventral median longitudinal folds.

"2. Separate narrow solid supports (radials), in longitudinal series, and with their long axes directed more or less outwards at right angles with the long axis of the body, were developed in varying extents in all these four longitudinal folds.

"3. The longitudinal folds became interrupted variously, but so as to form two prominences on each side, *i.e.* the primitive paired limbs.

"4. Each anterior paired limb increased in size more rapidly than the posterior limb.

"5. The bases of the cartilaginous supports coalesced as was needed, according to the respective practical needs of the different separate portions of the longitudinal folds, *i.e.* the respective needs of the several fins.

"6. Occasionally the dorsal radials coalesced (as in *Notidanus*, &c.) and sought centripetally (*Pristis*, &c.) adherence to the skeletal axis.

"7. The radials of the hinder paired limb did so more constantly, and ultimately prolonged themselves inwards by mesiad growth from their coalesced base, till the piscine pelvic structure arose, as *e.g.* in *Squatina*.

"8. The pectoral radials with increasing development also coalesced proximally, and thence prolonging themselves inwards to seek a *point d'appui*, shot dorsad and ventrad to obtain a firm support and at the same time to avoid the visceral cavity. Thus they came to abut dorsally against the axial skeleton, and to meet ventrally together in the middle line below.

"9. The lateral fins, as they were applied to support the body on the ground, became elongated, segmented, and narrowed, so that probably the line of the propterygium, or possibly that of the mesopterygium, became the cheiropterygial axis.

"10. The distal end of the incipient cheiropterygium either preserved and enlarged pre-existing cartilages or developed fresh ones to serve fresh needs, and so grew into the

---

[1] Loc. cit., p. 480.

developed cheiropterygium; but there is not yet enough evidence to determine what was the precise course of this transformation.

"11. The pelvic limb acquired a solid connection with the axial skeleton (a pelvic girdle) through its need of a *point d'appui* as a locomotive organ on land.

"12. The pelvic limb became also elongated; and when its function was quite similar to that of the pectoral limb, its structure became also quite similar (*e.g. Ichthyosaurus, Plesiosaurus, Chelydra,* &c.); but for the ordinary quadrupedal mode of progression it became segmented and inflected in a way generally parallel with, but (from its mode of use) in part inversely to, the inflections of the pectoral limb."

Günther[1] has propounded a theory on the primitive character of the fins, which, on the whole, fits in with the view that the paired fins are structures of the same nature as the unpaired fins. The interest of Günther's views on the nature of the skeleton of the fins more especially depends upon the fact that he attempts to evolve the fin of *Ceratodus* from the typical Selachian type of pectoral fin. His own statement on this subject is as follows:[2]

"On further inquiry into the more distant relations of the *Ceratodus*-limb we may perhaps be justified in recognizing in it a modification of the typical form of the Selachian pectoral fin. Leaving aside the usual treble division of the carpal cartilage (which, indeed, is sometimes simple), we find that this shovel-like carpal forms the base for a great number of phalanges, which are arranged in more or less regular transverse rows (zones) and in longitudinal rows (series). The number of phalanges of the zones and series varies according to the species and the form of the fin; in *Cestracion philippi* the greater number of phalanges is found in the proximal zones and middle series, all the phalanges decreasing in size from the base of the fin towards the margins. In a Selachian with a long, pointed, scythe-shaped, pectoral fin, like that of *Ceratodus,* we may, from analogy, presume that the arrangement of the cartilages might be somewhat like that shown in the accompanying diagram, which I have divided into nine zones and fifteen series.

"When we now detach the outermost phalanx from each side of the first horizontal zone, and with it the other phalanges of the same series, when we allow the remaining phalanges of this zone to coalesce into one piece (as, in nature, we find coalesced the carpels of *Ceratodus* and many

---

[1] "Description of *Ceratodus,*" 'Phil. Trans.,' 1871.

[2] Loc. cit., p. 534.

phalanges in Selachian fins), and when we repeat this same process with the following zones and outer series, we arrive at an arrangement identical with what we actually find in *Ceratodus*."

While the researches of Thacher and Mivart are strongly confirmatory of the view at which I had arrived with reference to the nature of the paired fins, other hypotheses as to the nature of the skeleton of the fins have been enunciated, both before and after the publication of my memoir, which are either directly or indirectly opposed to my view.

Huxley, in his memoir on *Ceratodus*, which throws light on so many important morphological problems, has dealt with the nature of paired fins.[1]

He holds, in accordance with a view previously adopted by Gegenbaur, that the limb of *Ceratodus* "presents us with the nearest approximation to the fundamental form of vertebrate limb or archipterygium," and is of opinion that in a still more archaic fish than *Ceratodus* the skeleton of the fin "would be made up of homologous segments, which might be termed pteromeres, each of which would consist of a mesomere with a preaxial and a postaxial paramere." He considers that the pectoral fins of Elasmobranchii, more especially the fin of *Notidanas*, which he holds to be the most primitive form of Elasmobranch fin, "results in the simplest possible manner from the shortening of the axis of such a fin-skeleton as that of *Ceratodus*, and the coalescence of some of its elements." Huxley does not enter into the question of the origin of the skeleton of the pelvic fin of Elasmobranchii.

It will be seen that Huxley's idea of the primitive structure of the archipterygium is not easily reconcilable with the view that the paired fins are parts of a once continuous lateral fin, in that the skeleton of such a lateral fin, if it has existed, must necessarily have consisted of a series of parallel rays.

Gegenbaur[2] has done much more than any other living

---

[1] T. H. Huxley, "On *Ceratodus Fosteri*, with some Observations on the Classification of Fishes," 'Proc. Zool. Soc.,' 1876.

[2] C. Gegenbaur, 'Untersuchungen z. vergleich. Anat. d. Wirbelthiere' (Leipzig, 1864-5): erstes Heft, Carpus u. Tarsus; zweites Heft, Brust flosse d. Fische.

"Ueb. d. Skelet d. Gliedmaassen d. Wirbelthiere im Allgemeinen u. d. Hintergliedmaassen d. Selachier insbesondere," 'Jenaische Zeitschrift,' vol. v, 1870.

"Ueb. d. Archipterygium," 'Jenaische Zeitschrift,' vol. vii, 1873.

"Zur Morphologie d. Gliedmaassen d. Wirbelthiere," 'Morphologisches Jahrbuch,' vol. ii, 1876.

anatomist to elucidate the nature of the fins; and his views on this subject have undergone considerable changes in the course of his investigations. After Günther had worked out the structure of the fin of *Ceratodus*, Gegenbaur suggested that it constituted the most primitive *persisting* type of fin, and has, moreover, formed a theory as to the origin of the fins founded on this view, to the effect that the fins, together with their respective girdles, are to be derived from visceral arches with their rays.

His views on this subject are clearly explained in the subjoined passages quoted from the English translation of his 'Elements of Comparative Anatomy,' pp. 473 and 477.

"The skeleton of the free appendage is attached to the extremity of the girdle. When simplest, this is made up of cartilaginous rods (rays), which differ in their size, segmentation, and relation to one another. One of these rays is larger than the rest, and has a number of other rays attached to its sides. I have given the name of *archipterygium* to the ground-form of the skeleton which extends from the limb-bearing girdle into the free appendage. The primary ray is the stem of this archipterygium, the characters of which enable us to follow out the lines of development of the skeleton of the appendage. Cartilaginous arches beset with the rays form the branchial skeleton. The form of skeleton of the appendages may be compared with them; and we are led to the conclusion that it is possible that they may have been derived from such forms. In the branchial skeleton of the Selachii the cartilaginous bars are beset with simple rays. In many a median one is developed to a greater size. As the surrounding rays become smaller, and approach the larger one we get an intermediate step towards that arrangement in which the larger median ray carries a few smaller ones. This differentiation of one ray, which is thereby raised to a higher grade, may be connected with the primitive form of the appendicular skeleton; and as we compare the girdle with a branchial arch, so we may compare the median ray and its secondary investment of rays with the skeleton of the free appendage.

"All the varied forms which the skeleton of the free appendages exhibits may be derived from a ground-form which persists in a few cases only, and which represents the first, and consequently the lowest, stage of the skeleton in the fin—the *archipterygium*. This is made up of a stem which consists of jointed pieces of cartilage, which is articulated to the shoulder-girdle and is beset on either side with rays which are likewise jointed. In addition to the rays of the stem there are others which are directly attached to the limb-girdle.

"*Ceratodus* has a fin-skeleton of this form; in it there is a stem beset with two rows of rays. But there are no rays in the shoulder-girdle. This biserial investment of rays on the stem of the fin may also undergo various kinds of modifications. Among the Dipnoi, *Protopterus* retains the medial row of rays only, which have the form of fine rods of cartilage; in the Selachii, on the other hand, the lateral rays are considerably developed. The remains of the medial row are ordinarily quite small, but they are always sufficiently distinct to justify us in supposing that in higher forms the two sets of rays might be better developed. Rays are still attached to the stem and are connected with the shoulder-girdle by means of larger plates. The joint of the rays are sometimes broken up into polygonal plates, which may further fuse with one another; concrescence of this kind may also affect the pieces which form the base of the fin. By regarding the free rays, which are attached to these basal pieces, as belonging to these basal portions, we are able to divide the entire skeleton of the fin into three segments—pro-, meso-, and metapterygium.

"The metapterygium represents the stem of the archipterygium and the rays on it. The propterygium and the mesopterygium are evidently derived from the rays which still remain attached to the shoulder-girdle."

Since the publication of the memoirs of Thacher, Mivart, and myself, a pupil of Gegenbaur's, M. v. Davidoff,[1] has made a series of very valuable observations, in part directed towards demonstrating the incorrectness of our theoretical views, more especially Thacher's and Mivart's view of the genesis of the skeleton of the limbs. Gegenbaur[2] has also written a short paper in connection with Davidoff's memoir, in support of his own as against our views.

It would not be possible here to give an adequate account of Davidoff's observations on the skeleton, muscular system, and nerves of the pelvic fins. His main argument against the view that the paired fins are the remains of a continuous lateral fin is based on the fact that a variable but often considerable number of the spinal nerves in front of the pelvic fin are united by a longitudinal commissure with the true plexus of the nerves supplying the fin. From this he

---

[1] M. v. Davidoff, "Beiträge z. vergleich. Anat. d. hinteren Gliedmaassen d. Fische I.," 'Morphol. Jahrbuch,' vol. v, 1879.

[2] "Zur Gliedmaassenfrage. An die Untersuchungen von Davidoff's angeknüpfte Bemerkungen," 'Morphol. Jahrbuch,' vol. v, 1879.

concludes that the pelvic fin has shifted its position, and that it may once therefore have been situated close behind the visceral arches. Granting, however, that Davidoff's deduction from the character of the pelvic plexus is correct, there is, so far as I see, no reason in the nature of the lateral-fin theory why the pelvic fins should not have shifted; and, on the other hand, the longitudinal cord connecting some of the ventral roots in front of the pelvic fin may have another explanation. It may, for instance, be a remnant of the time when the pelvic fin had a more elongated form than at present, and accordingly extended further forwards.

In any case our knowledge of the nature and origin of nervous plexuses is far too imperfect to found upon their characters such conclusions as those of Davidoff.

Gegenbaur, in his paper above quoted, further urges against Thacher's and Mivart's views the fact that there is no proof that the fin of *Polyodon* is a primitive type; and also suggests that the epithelial line which I have found connecting the embryonic pelvic and pectoral fins in *Torpedo* may be a rudiment indicating a migration backwards of the pelvic fin.

With reference to the development of the pectoral fin in the Teleostei, there are some observations of 'Swirski,[1] which unfortunately do not throw very much light upon the nature of the limb.

'Swirski finds that in the Pike the skeleton of the limb is formed of a plate of cartilage continuous with the pectoral girdle, which soon becomes divided into a proximal and a distal portion. The former is subsequently segmented into five basal rays, and the later into twelve parts, the number of which subsequently becomes reduced.

The observations recorded in the present paper were made with the object of determining how far the development of the skeleton of the limbs throws light on the points on which the anatomists whose opinions have just been quoted are at variance.

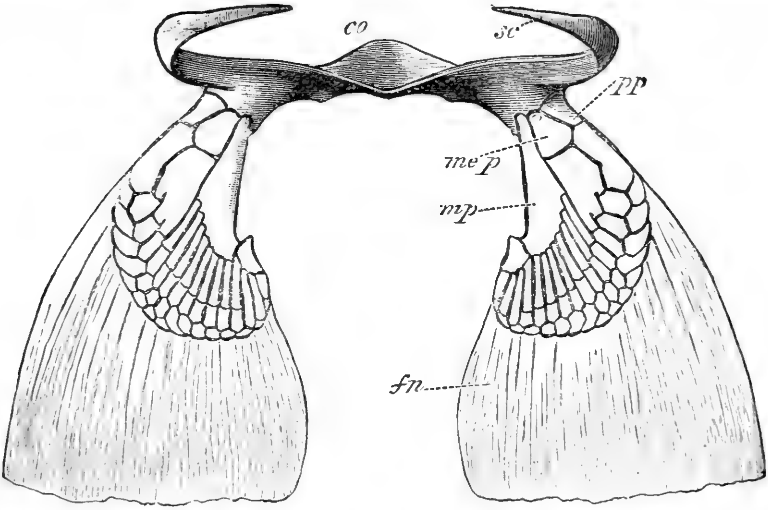
They were made, in the first instance, to complete a chapter in my work on comparative embryology; and, partly owing to the press of other engagements, but still more to the difficulty of procuring material, my observations are confined to the two British species of the genus *Scyllium*, viz. *Sc. stellare* and *Sc. canicula*; yet I venture to believe that the results at which I have arrived are not wholly without interest.

---

[1] G. 'Swirski, 'Untersuch. üb. d. Entwick. d. Schultergurtels u. d. Skelets d. Brustflosse d. Hechts.,' Inaug. Diss., Dorpat, 1880.

Before dealing with the development of the skeleton of the fin, it will be convenient to describe with great brevity the structure of the pectoral and pelvic fins of the adult. The pectoral fins consist of broad plates inserted horizontally on the sides of the body; so that in each there may be distinguished a dorsal and a ventral surface, and an anterior and a posterior border. Their shape may best be gathered from the woodcut (fig. 1); and it is to be especially noted that the narrowest part of the fin is the base, where it is attached to the side of the body. The cartilaginous skeleton

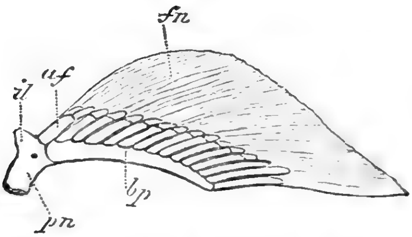
Fig. 1.



Pectoral fins and girdle of an adult of *Scyllium canicula* (natural size, seen from behind and above.)

co. Coracoid; *sc.* scapula; *pp.* propterygium; *me p.* mesopterygium; *mp.* metapterygium; *fn.* part of fin supported by horny fibre.

Fig. 2.



Right pelvic fin and part of pelvic girdle of an adult female of *Scyllium canicula* (natural size).

il. Iliac process; *pn.* pubic process, cut across below; *bp.* basipterygium; *af.* anterior cartilaginous fin-ray articulated to pelvic girdle; *fn.* part of fin supported by horny fibres.

only occupies a small zone at the base of the fin, the remainder being formed of a fringe supported by radiately arranged horny fibres.[1]

The true skeleton consists of three basal pieces articulating with the pectoral girdle; on the outer side of which there is a series of more or less segmented cartilaginous fin-rays. Of the basal cartilages one (*pp*) is anterior, a second (*mep*) is placed in the middle, and a third is posterior (*mp*). They have been named by Gegenbaur the *propterygium,* the *mesopterygium,* and the *metapterygium ;* and these names are now generally adopted.

The metapterygium is by far the most important of the three, and in *Scyllium canicula* supports twelve or thirteen rays.[2] It forms a large part of the posterior boundary of the fin, and bears rays only on its *anterior* border.

The mesopterygium supports two or three rays, in the basal parts of which the segmentation into distinct rays is imperfect; and the propterygium supports only a single ray.

The pelvic fins are horizontally placed, like the pectoral fins, but differ from the latter in nearly meeting each other along the median ventral line of the body. They also differ from the pectoral fins in having a relatively much broader base of attachment to the sides of the body. Their cartilaginous skeleton (woodcut, fig. 2) consists of a basal bar, placed parallel to the base of the fin, and articulated in front with the pelvic girdle.

On its outer border it articulates with a series of cartilaginous fin-rays. I shall call the basal bar the basipterygium. The rays which it bears are most of them less segmented than those of the pectoral fin, being only divided into two; and the posterior ray, which is placed in the free posterior border of the fin, continues the axis of the basipterygium. In the male it is modified in connection with the so-called clasper.

The anterior fin-ray of the pelvic fin, which is broader than the other rays, articulates directly with the pelvic girdle, instead of with the basipterygium. This ray, in the female of *Scyllium canicula* and in the male of *Scyllium catulus* (Gegenbaur), is peculiar in the fact that its distal segment is longitudinally divided into two or more pieces, instead of

---

[1] The horny fibres are mesoblastic products; they are formed, in the first instance, as extremely delicate fibrils on the inner side of the membrane separating the epiblast from the mesoblast.

[2] In one example where the metapterygium had 13 rays the mesopterygium had only 2 rays.

being single as is the case with the remaining rays. It is probably equivalent to two of the posterior rays.

Development of the paired Fins.—The first rudiments of the limbs appear in *Scyllium*, as in other fishes, as slight longitudinal ridge-like thickenings of the epiblast, which closely resemble the first rudiments of the unpaired fins.

These ridges are two in number on each side—an anterior immediately behind the last visceral fold, and a posterior on the level of the cloaca. In most Fishes they are in no way connected; but in some Elasmobranch embryos, more especially in that of *Torpedo*, they are connected together at their first development by a line of columnar-epiblast cells. This connecting line of columnar epiblast, however, is a very transitory structure. The rudimentary fins soon become more prominent, consisting of a projecting ridge both of epiblast and mesoblast, at the outer edge of which is a fold of epiblast only, which soon reaches considerable dimensions. At a later stage the mesoblast penetrates into this fold, and the fin becomes a simple ridge of mesoblast covered by epiblast. The pectoral fins are at first considerably ahead of the pelvic fins in development.

The direction of the original epithelial line which connected the two fins of each side is nearly, though not quite, longitudinal, sloping somewhat obliquely ventralwards. It thus comes about that the attachment of each pair of limbs is somewhat on a slant, and that the pelvic pair nearly meet each other in the median ventral line shortly behind the anus.

The embryonic muscle-plates, as I have elsewhere shown, grow into the bases of the fins; and the cells derived from these ingrowths, which are placed on the dorsal and ventral surfaces in immediate contact with the epiblast, probably give rise to the dorsal and ventral muscular layers of the limb, which are shown in section in Plate IV, fig. 1 *m* and in Plate V, fig. 7 *m*.

The cartilaginous skeleton of the limbs is developed in the indifferent mesoblast cell between the two layers of muscles. Its early development in both the pectoral and the pelvic fins is very similar. When first visible it differs histologically from the adjacent mesoblast simply in the fact of its cells being more concentrated; while its boundary is not sharply marked.

At this stage it can only be studied by means of sections. It arises simultaneously and continuously with the pectoral and pelvic girdles, and consists, in both fins, of a bar springing at right angles from the posterior side of the pectoral or pelvic girdle, and running parallel to the long axis of the body along the base of the fin. The outer side of this bar is continued into a thin plate, which extends into the fin.

The structure of the skeleton of the fin slightly after its first differentiation will be best understood from Plate IV, fig. 1, and Plate V, fig. 7. These figures represent transverse sections through the pelvic and pectoral fins of the same embryo on the same scale. The basal bar is seen at *bp*, and the plate at this stage (which is considerably later than the first differentiation) already partially segmented into rays at *br*. Outside the region of the cartilaginous plate is seen the fringe with the horny fibres (*h.f*); and dorsally and ventrally to the cartilaginous skeleton are seen the already well-differentiated muscles (*m*).

The pectoral fin is shown in horizontal section in Plate V, fig. 6, at a somewhat earlier stage than that to which the transverse sections belong. The pectoral girdle (*p.g*) is cut transversely, and is seen to be perfectly continuous with the basal bar (*bp*) of the fin. A similar continuity between the basal bar of the pelvic fin and the pelvic girdle is shown in Plate IV, fig. 2, at a somewhat later stage. The plate continuous with the basal bar of the fin is at first, to a considerable extent in the pectoral, and to some extent in the pelvic fin, a continuous lamina, which subsequently segments into rays. In the parts of the plate which eventually form distinct rays, however, almost from the first the cells are more concentrated than in those parts which will form the tissue between the rays; and I am not inclined to lay any stress whatever upon the fact of the cartilaginous fin-rays being primitively part of a continuous lamina, but regard it as a secondary phenomenon, dependent on the mode of conversion of embryonic mesoblast cells into cartilage. In all cases the separation into distinct rays is to a large extent completed before the tissue of which the plates are formed is sufficiently differentiated to be called cartilage by an histologist.

The general position of the fins in relation to the body, and their relative sizes, may be gathered from Plate IV, figs. 4 and 5, which represent transverse sections of the same embryo as that from which the tranverse sections showing the fin on the larger scale were taken.

During the first stage of its development the skeleton of both fins may thus be described as consisting of *a longitudinal bar running along the base of the fin, and giving off at right angles series of rays which pass into the fin.* The longitudinal bar may be called the basipterygium; and it is continuous in front with the pectoral or pelvic girdle, as the case may be.

The further development of the primitive skeleton is different in the case of the two fins.

The Pelvic Fin.—The changes in the pelvic fin are comparatively slight. Plate IV, fig. 2 is a representation of the fin and its skeleton in a female of *Scyllium stellare* shortly after the primitive tissue is converted into cartilage, but while it is still so soft as to require the very greatest care in dissection. The fin itself forms a simple projection of the side of the body. The skeleton consists of a basipterygium (*bp*), continuous in front with the pelvic girdle. To the outer side of the basipterygium a series of cartilaginous fin-rays are attached—the posterior ray forming a direct prolongation of the basipterygium, while the anterior ray is united rather with the pelvic girdle than with the basipterygium. All the cartilaginous fin-rays except the first are completely continuous with the basipterygium, their structure in section being hardly different from that shown in Plate IV, fig. 1.

The external form of the fin does not change very greatly in the course of the further development; but the hinder part of the attached border is, to some extent, separated off from the wall of the body, and becomes the posterior border of the adult fin. With the exception of a certain amount of segmentation in the rays, the character of the skeleton remains almost as in the embryo. The changes which take place are illustrated by Plate IV, fig. 3, showing the fin of a young male of *Scyllium stellare.* The basipterygium has become somewhat thicker, but is still continuous in front with the pelvic girdle, and otherwise retains its earlier characters. The cartilaginous fin-rays have now become segmented off from it and from the pelvic girdle, the posterior end of the basiterygial bar being segmented off as the terminal ray.

The anterior ray is directly articulated with the pelvic girdle, and the remaining rays continue articulated with the basipterygium. Some of the latter are partially segmented.

As may be gathered by comparing the figure of the fin at the stage just described with that of the adult fin (woodcut, fig. 2), the remaining changes are very slight. The most important is the segmentation of the basipterygial bar from the pelvic girdle.

The pelvic fin thus retains in all essential points its primitive structure.

The *Pectoral Fin.*—The earliest stage of the pectoral fin differs, as I have shown, from that of the pelvic fin only in minor points (Plate V, fig. 6). There is the same longitudinal or basipterygial bar (*bp*), to which the fin-rays are attached, which is continuous in front with the pectoral girdle (*p g*). The changes which take place in the course of the further development, however, are very much more considerable in the case of the pectoral that in that of the pelvic fin.

The most important change in the external form of the fin is caused by a reduction in the length of its attachments to the body. At first (Plate V, fig. 6), the base of the fin is as long as the greatest breadth of the fin; but it gradually becomes shortened by being constricted off from the body at its hinder end. In connection with this process the posterior end of the basipterygial bar is gradually rotated outwards, its anterior end remaining attached to the pectoral girdle. In this way this bar comes to form the posterior border of the skeleton of the fin (Plate V, figs. 8 & 9), constituting the metapterygium (*mp*). It becomes eventually segmented off from the pectoral girdle, simply articulating with its hinder edge.

The plate of cartilage, which is continued outwards from the basipterygium, or, as we may now call it, the metapterygium, into the fin, is not nearly so completely divided up into fin-rays as the homologous part of the pelvic fin; and this is especially the case with the basal part of the plate. This basal part becomes, in fact, at first only divided into two parts (Plate V, fig. 8)—a small anterior part at the front end (*me.p*), and a larger posterior along the base of the metapterygium (*mp*); and these two parts are not completely segmented from each other. The anterior part directly joins the pectoral girdle at its base, resembling in this respect the anterior fin-ray of the pelvic girdle. It constitutes the (at this stage undivided) rudiment of the mesopterygium and propterygium of Gegenbaur. It bears in my specimen of this age four fin-rays at its extremity, the anterior not being well marked. The remaining fin-rays are prolongations outwards of the edge of the plate continuous with the metapterygium. These rays are at the stage figured more or less transversely segmented, but at their outer edge they are united together by a nearly continuous rim of cartilage. The spaces between the fin-rays are relatively considerably larger than in the adult.

The further changes in the cartilages of the pectoral limb are, morphologically speaking, not important, and are easily understood by reference to Plate V, fig. 9 (representing the skeleton of the limb of a nearly ripe embryo). The front end of the anterior basal cartilage becomes segmented off as a propterygium (*pp*), bearing a single fin-ray, leaving the remainder of the cartilage as a mesopterygium (*mes*). The remainder of the now considerably segmented fin-rays are borne by the metapterygium.

General Conclusions.—From the above observations, conclusions of a positive kind may be drawn as to the primitive structure of the skeleton; and the observations have also, it appears to me, important bearings on the theories of my predecessors in this line of investigation.

The most obvious of the positive conclusions is to the effect that the embryonic skeleton of the paired fins consists of a series of parallel rays similar to those of the unpaired fins. These rays support the soft parts of the fins, which have the form of a longitudinal ridge; and they are continuous at their base with a longitudinal bar. This bar, from its position at the base of the fin, can clearly never have been a medium axis with the rays on both sides. It becomes the basipterygium in the pelvic fin, which retains its embryonic structure much more completely than the pectoral fin; and the metapterygium in the pectoral fin. The metapterygium of the pectoral fin is thus clearly homologous with the basipterygium of the pelvic fin, as originally supposed by Gegenbaur, and has since been maintained by Mivart. The propterygium and mesopterygium are obviously relatively *unimportant* parts of the skeleton as compared with the metapterygium.

My observations on the development of the skeleton of fins certainly do not of themselves demonstrate that the paired fins are remnants of a once continuous lateral fin; but they support this view in that they show the primitive skeleton of the fins to have exactly the character which might have been anticipated if the paired fins had originated from a continuous lateral fin. The longitudinal bar of the paired fins is believed by both Thacher and Mivart to be due to the coalescence of the bases of the primitively independent rays of which they believe the fin to have been originally composed. This view is probable enough in itself, and is rendered more so by the fact, pointed out by Mivart, that a longitudinal bar supporting the cartilaginous rays or unpaired fins is occasionally formed; but there is no trace in the embryos of the Scyllium of the bar in question being formed by the coalescence of rays, though the fact of its being perfectly continuous with the basis of the fin-rays is somewhat in favour of such coalescence.

Thacher and Mivart both hold that the pectoral and pelvic girdles are developed by ventral and dorsal growths of the anterior end of the longitudinal bar supporting the fin-rays.

There is, so far as I see, no theoretical objection to be taken to this view; and the fact of the pectoral and pelvic girdles originating continuously and long remaining united with the longitudinal bars of their respective fins is in favour of it rather than the reverse. The same may be said of the fact that the first part of each girdle to be formed is that in the neighbourhood of the longitudinal bar (basipterygium) of the fin, the dorsal and ventral prolongations being subsequent growths.

On the whole my observations do not throw much light on the theories of Thacher and Mivart as to the genesis of the skeleton of the paired fin; but, so far as they bear on the subject, they are distinctly favorable to those theories.

The main results of my observations appear to me to be decidedly adverse to the views recently put forward on the structure of the fin by Gegenbaur and Huxley, both of whom, as stated above, consider the primitive type of fin to be most nearly retained in *Ceratodus*, and to consist of a central multisegmented axis with numerous lateral rays.

Gegenbaur derives the Elasmobranch pectoral fin from a form which he calls the archipterygium, nearly like that of *Ceratodus*, with a median axis and two rows of rays—but holds that in addition to the rays attached to the median axis, which are alone found in *Ceratodus*, there were other rays directly articulated to the shoulder-girdle. He considers that in the Elasmobranch fin the majority of the lateral rays on the posterior (or median according to his view of the position of the limb) side have become aborted, and that the central axis is represented by the metapterygium; while the pro- and mesopterygium and their rays are, he believes, derived from those rays of the archipterygium which originally articulated directly with the shoulder-girdle.

This view appears to me to be absolutely negatived by the facts of development of the pectoral fin in *Scyllium*—not so much because the pectoral fin in this form is necessarily to be regarded as primitive, but because what Gegenbaur holds to be the primitive axis of the biserial fin is demonstrated to be really the base, and it is only in the adult that it is conceivable that a second set of lateral rays could have existed on the posterior side of the metapterygium. If Gegenbaur's view were correct, we should expect to find in the embryo, if anywhere, traces of the second set of lateral rays; but the fact is that, as may easily be seen by an inspection of figs 6 and 7, such a second set of lateral rays could not possibly have existed in a type of fin like that found in the embryo. With this view of Gegenbaur's it appears to me that the theory held by this anatomist to the effect that the limbs are modified gill-arches also falls, in that his method of deriving the limbs from gill-arches ceases to be admissible, while it is not easy to see how a limb, formed on the type of the embryonic limb of Elasmobranchs, could be derived from a gill-arch with its branchial rays.

Gegenbaur's older view, that the Elasmobranch fin retains a primitive uniserial type, appears to me to be nearer the truth than his more recent view on this subject; though I hold the fundamental point established by the development of these parts in *Scyllium* to be that the posterior border of the adult Elasmobranch pectoral fin is the primitive base-line, *i e.* line of attachment of the fin to the side of the body.

Huxley holds that the mesopterygium is the proximal piece of the axial skeleton of the limb of *Ceratodus,* and derives the Elasmobranch fin from that of *Ceratodus* by the shortening of its axis and the coalescence of some of its elements. The entirely secondary character of the mesopterygium, and its total absence in the young embryo *Scyllium,* appear to me as conclusive against Huxley's view as the character of the embryonic fin is against that of Gegenbaur; and I should be much more inclined to hold that the fin of *Ceratodus* has been derived from a fin like that of the Elasmobranchs by a series of steps similar to those which Huxley supposes to have led to the establishment of the Elasmobranch fin, but in exactly the reverse order.

There is one statement of Davidoff's which I cannot allow to pass without challenge. In comparing the skeletons of the paired and unpaired fins he is anxious to prove that the former are independent of the axial skeleton in their origin, and that the latter have been segmented from the axial skeleton, and thus to show that an homology between the two is impossible. In support of his view he states[1] that he has satisfied himself, from embryos of *Acanthias* and *Scyllium,* that the rays of the unpaired fins *are undoubtedly products of the segmentation of the dorsal and ventral spinous processes.*

This statement is wholly unintelligible to me.[2] From my examination of the development of the first dorsal and the

---

[1] Loc. cit., p. 514.

[2] It is possible that Davidoff may have only studied the ventral lobe of the caudal fin, which differs from the other unpaired fins in the fact that there are no interspinous elements supporting the horny fin-rays.

anal fins of *Scyllium* I find that their cartilaginous rays develop at a considerable distance from, and quite independently of, the neural and hæmal arches, and that they are at an early stage of development distinctly in a more advanced state of histological differentiation than the neural and hæmal arches of the same region. I have also found exactly the same in the embryos of *Lepidosteus.*

I have, in fact, no doubt that the skeleton of both the paired and the unpaired fins of Elasmobranchs and *Lepidosteus* is in its development independent of the axial skeleton. The phylogenetic mode of origin of the skeleton both of the paired and of the unpaired fins cannot, however, be made out without further investigation.

On the NATURE *of the* ORGAN *in* ADULT TELEOSTEANS *and* GANOIDS, *which is usually regarded as the* HEAD-KIDNEY *or* PRONEPHROS. By F. M. BALFOUR, LL.D., F.R.S., Fellow of Trinity College, Cambridge.

WHILE working at the anatomy of Lepidosteus I was led to doubt the accuracy of the accepted accounts of the anterior part of the kidneys in this and in allied species of Fishes. In order to test my doubts I first examined the structure of the kidneys in the Sturgeon (Acipenser), of which I fortunately had a well-preserved specimen.

The bodies usually described as the kidneys consist of two elongated bands, attached to the dorsal wall of the abdomen, and extending for the greater part of the length of the abdominal cavity. In front each of these bands first becomes considerably narrowed, and then expands and terminates in a great dilatation, which is usually called the head-kidney. Along the outer border of the hinder part of each kidney is placed a wide ureter, which ends suddenly in the narrow part of the body, some little way behind the head-kidney. To the naked eye there is no distinction in structure between the part of the so-called kidney in front of the ureter and that in the region of the ureter. Any section through the kidney in the region of the ureter suffices to show that in this part the kidney is really formed of uriniferous tubuli with numerous Malpighian bodies. Just in front, however, of the point where the ureter ends the true kidney substance rapidly thins out, and its place is taken by a peculiar tissue formed of a trabecular work filled with cells, which I shall in future call lymphatic tissue. *Thus the whole of that part of the apparent kidney in front of the ureter, including the whole of the so-called head-kidney, is simply a great mass of lymphatic tissue, and does not contain a single uriniferous tubule or Malpighian body.*

The difference in structure between the anterior and posterior parts of the so-called kidney, although not alluded to in most modern works on the kidneys, appears to have been known to

Stannius, at least I so interpret a note of his in the second edition of his 'Comparative Anatomy,' p. 263, where he describes the kidney of the Sturgeon as being composed of two separate parts, viz. a spongy vascular substance (no doubt the so-called head-kidney) and a true secretory substance.

After arriving at the above results with reference to the Sturgeon I proceeded to the examination of the structure of the so-called head-kidney in Teleostei.

I have as yet only examined four forms, viz. the Pike (*Esox lucius*), the Smelt (*Osmerus eperlanus*), the Eel (*Anguilla anguilla*), and the Angler (*Lophius piscatorius*).

The external features of the apparent kidney of the Pike have been accurately described by Hyrtl.[1] He says: "The kidneys extend from the second trunk vertebra to the end of the abdominal cavity. Their anterior extremities, which have the form of transversely placed coffee beans, are united together, and lie on the anterior end of the swimming bladder. The continuation of the kidney backwards forms two small bands, separated from each other by the whole breadth of the vertebral column. They gradually, however, increase in breadth, so that about the middle of the vertebral column they unite together and form a single symmetrical, keel-shaped body," &c.

The Pike I examined was a large specimen of about 58 centimètres in length, and with an apparent kidney of about 25½ centimètres. The relations of lymphatic tissue and kidney tissue were much as in the Sturgeon. The whole of the anterior swelling, forming the so-called head-kidney, together with a considerable portion of the part immediately behind, forming not far short of half the whole length of the apparent kidney, was entirely formed of lymphatic tissue. The posterior part of the kidney was composed of true kidney substance, but even at 16 centimètres from the front end of the kidney the lymphatic tissue formed a large portion of the whole.

A rudiment of the duct of the kidney extended forwards for a short way into the lymphatic substance beyond the front part of the functional kidney.

In the Smelt (*Osmerus eperlanus*) the kidney had the typical Teleostean form, consisting of two linear bands stretching for the whole length of the body-cavity, and expanding into a great swelling in front on the level of the ductus Cuvieri, forming the so-called head-kidney. The histological examination of these bodies showed generally the same features as in the case of the Sturgeon and Pike. The posterior part was formed of the usual uriniferous tubuli and Malpighian bodies. The anterior

---

[1] "Das Uropoëtische System d. Knochenfische," Sitz. d. 'Wien. Akad.,' 1850.

swollen part of these bodies, and the part immediately following, were almost wholly formed of a highly vascular lymphatic tissue; but in a varying amount in different examples portions of uriniferous tubules were present, mainly, however, in the region behind the anterior swelling. In some cases I could find no tubules in the lymphatic tissue, and in all cases the number of them beyond the region of the well-developed part of the kidney was so slight, that there can be little doubt that they are functionless remnants of the anterior part of the larval kidney. Their continuation into the anterior swelling, when present, consisted of a single tube only.

In the Eel (*Anguilla anguilla*), which, however, I have not examined with the same care as the Smelt, the true excretory part of the kidney appears to be confined to the posterior portion, and to the portion immediately in front of the anus, the whole of the anterior part of each apparent kidney, which is not swollen in front, being composed of lymphatic tissue.

Lophius piscatorius is one of the forms which, according to Hyrtl,[1] is provided with a head-kidney only, *i. e.* with that part of the kidney which corresponds with the anterior swelling of the kidney of other types. For this reason I was particularly anxious to investigate the structure of its kidneys.

Each of these bodies forms a compact oval mass, with the ureter springing from its hinder extremity, situated in a forward position in the body cavity. Sections through the kidneys showed that they were throughout penetrated by uriniferous tubules, but owing to the bad state of preservation of my specimens I could not come to a decision as to the presence of Malpighian bodies. The uriniferous tubules were embedded in lymphatic tissue, similar to that which forms the anterior part of the apparent kidneys in other Teleostean types.

With reference to the structure of the Teleostean kidneys, the account given by Stannius is decidedly more correct than that of most subsequent writers. In the note already quoted he gives it as his opinion that there is a division of the kidney into the same two parts as in the Sturgeon, viz. into a spongy vascular part and a true secreting part; and on a subsequent page he points out the absence or poverty of the uriniferous tubules in the anterior part of the kidney in many of our native Fishes.

Prior to the discovery that the larvæ of Teleosteans and Ganoids were provided with two very distinct excretory organs, viz. a pronephros or head-kidney, and a mesonephros or Wolffian body, which are usually separated from each other by a more or less considerable interval, it was a matter of no very great im-

---

[1] "Das Uropoetische System de Knochenfische," 'Sitz. d. Wien. Akad.' 1850.

portance to know whether the anterior part of the so-called kidney was a true excretory organ. In the present state of our knowledge the question is, however, one of considerable interest.

In the Cyclostomata and Amphibia the pronephros is a purely larval organ, which either disappears or ceases to be functionally active in the adult state.

Rosenberg, to whom the earliest satisfactory investigations on the development of the Teleostean pronephros are due, stated that he had traced in the Pike (*Esox lucius*) the larval organ into the adult part of the kidney, called by Hyrtl the pronephros; and subsequent investigators have usually assumed that the so-called head-kidney of adult Teleosteans and Ganoids is the persisting larval pronephros.

We have already seen that Rosenberg was entirely mistaken on this point, in that the so-called head-kidney of the adult is not part of the true kidney. From my own studies on young Fishes I do not believe that the oldest larvæ investigated by Rosenberg were sufficiently advanced to settle the point in question; and, moreover, as Rosenberg had no reason for doubting that the so-called head-kidney of the adult was part of the excretory organ, he does not appear to have studied the histological structure of the organ which he identified with the embryonic pronephros in his oldest larva.

The facts to which I have called attention in this paper demonstrate that in the Sturgeon the larval pronephros undoubtedly undergoes atrophy before the adult stage is reached. The same is true for Lepidosteus, and may probably be stated for Ganoids generally.

My observations on Teleostei are clearly not sufficiently extensive to *prove* that the larval pronephros *never* persists in this group. They appear to me, however, to show that in the normal types of Teleostei the organ usually held to be the pronephros is actually nothing of the kind.

A different interpretation might no doubt be placed upon my observations on *Lophius piscatorius*, but the position of the kidney in this species appears to me to be far from affording a conclusive proof that it is homologous with the anterior swelling of the kidney of more normal Teleostei.

When, moreover, we consider that Lophius, and the other forms mentioned by Hyrtl as being provided with a head-kidney only, are all of them peculiarly modified and specialised types of Teleostei, it appears to me far more natural to hold that their kidney is merely the ordinary Teleostean kidney, which, like many of their other organs, has become shifted in position, than to maintain that the ordinary excretory organ present in other

Teleostei has been lost, and that a larval organ has been retained, which undergoes atrophy in less specialised Teleostei.

As the question at present stands, it appears to me that the probabilities are in favour of there being no functionally active remains of the pronephros in adult Teleostei, and that in any case the burden of proof rests with those who maintain that such remnants are to be found.

The general result of my investigations is thus to render it probable *that the pronephros, though found in the larvæ or embryos of almost all the Ichthyopsida, except the Elasmobranchii, is always a purely larval organ, which never constitutes an active part of the excretory system in the adult state.*

This conclusion appears to me to add probability to the view of Gegenbaur that the pronephros is the primitive excretory gland of the Chordata; and that the mesonephros or Wolffian body, by which it is replaced in existing Ichthyopsida, is phylogenetically a more recent organ.

In the preceding pages I have had frequent occasion to allude to the lymphatic tissue which has been usually mistaken for part of the excretory organ. This tissue is formed of trabecular work, like that of lymphatic glands, in the meshes of which an immense number of cells are placed, which may fairly be compared with the similarly placed cells of lymphatic glands. In the Sturgeon a considerable number of cells are found with peculiar granular nuclei, which are not found in the Teleostei. In both groups, but especially in the Teleostei, the tissue is highly vascular, and is penetrated throughout by a regular plexus of very large capillaries, which appear to have distinct walls, and which pour their blood into the posterior cardinal vein as it passes through the organ. The relation of this tissue to the lymphatic system I have not made out.

The function of the tissue is far from clear. Its great abundance, highly vascular character, and presence before the atrophy of the pronephros, appear to me to show that it cannot be merely the non-absorbed remnant of the latter organ. From its size and vascularity it probably has an important function; and from its structure this most either be the formation of lymph corpuscles or of blood corpuscles.

In structure it most resembles a lymphatic gland, though, till it has been shown to have some relation to the lymphatic system, this can go for very little.

On the whole, I am provisionally inclined to regard it as a form of lymphatic gland, these bodies being not otherwise represented in fishes.

EXPLANATION OF PLATE VI,

Illustrating Mr. K. Mitsukuri's Paper on the "Development of the Suprarenal Bodies in Mammalia."

Explanation of Figures.

The outlines of all the figures, except Fig. 10, are drawn with Zeiss's obj. A and camera lucida with eye-piece 4, and then reduced one-third, except Fig. 1. Fig .10 is drawn with Zeiss's obj. a and the same camera lucida.

General Letters of Reference.

Ao. Aorta. *c.* Cortical part of the suprarenal bodies. *ch.* Notochord. *m.* Medullary part of the suprarenal. *n.* Peripheral sympathetic part with ganglion cells. *p.* Peripheral sympathetic part without ganglion cells. *p. p.* Body cavity. *s. r.* Suprarenal bodies. *symp.* Sympathetic cords. *v* .Viens. *v. c.* Cardinal veins. *v. c. i.* Vena cava inferior. *W.b.* Wolffian body.

FIG. 1.—A part of the transverse section of the adult suprarenal body of the rabbit.

d. Capsule. *a.* The outermost zone of the cortex. *b.* Zona fasciculata. *c.* Zona reticulatis. *w. w.* Blood-cavities.

FIG. 2.—A longitudinal section of the posterior end of the adult suprarenal body of the rabbit. The upper end of the figure is posterior.

a. Cells like ganglion cells. *b.* A place where one of the irregular cords of cells taper and seem to pass off into nerve fibres. *d.* Blood-capillaries. *g.* Ganglion-like mass. *i.* Blood-vessel. *y.* Nerve-bundle.

FIG. 3.—Section from a rabbit embryo twelve days old.

FIG. 4.—Section from a rabbit embryo fourteen days old.

g. Germinal band.

FIG. 5.—Section from a rabbit embryo sixteen days old.

a. Nervous fibres given off from the mass *n.*

FIG. 6.—Section immediately behind that represented in Fig. 5 from the same embryo.

FIG. 7.—Section of the right suprarenal from a rat embryo 23 mm. long.

b. Nervous bundles entering the suprarenal.

FIG. 8.—Section of the suprarenal from an embryo rabbit twenty-six days old, near the middle of the organ.

FIG. 9.—Ditto, near the posterior end. The outer part of the suprarenal is torn away.

a. Nervous bundle.

FIG. 10.—Series of diagrammatic longitudinal sections of the suprarenal from an embryo rabbit twenty-four days old.

A is the furthest from and D the nearest to the median axis of the body of the embryo. Between A and B there is one section. B and C are consecutive. Between C and D there are two sections. In each figure the upper end is anterior and the right side dorsal.

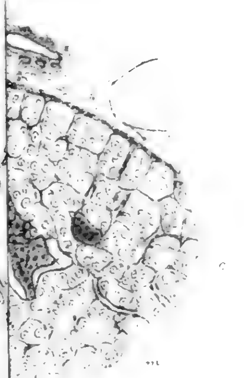
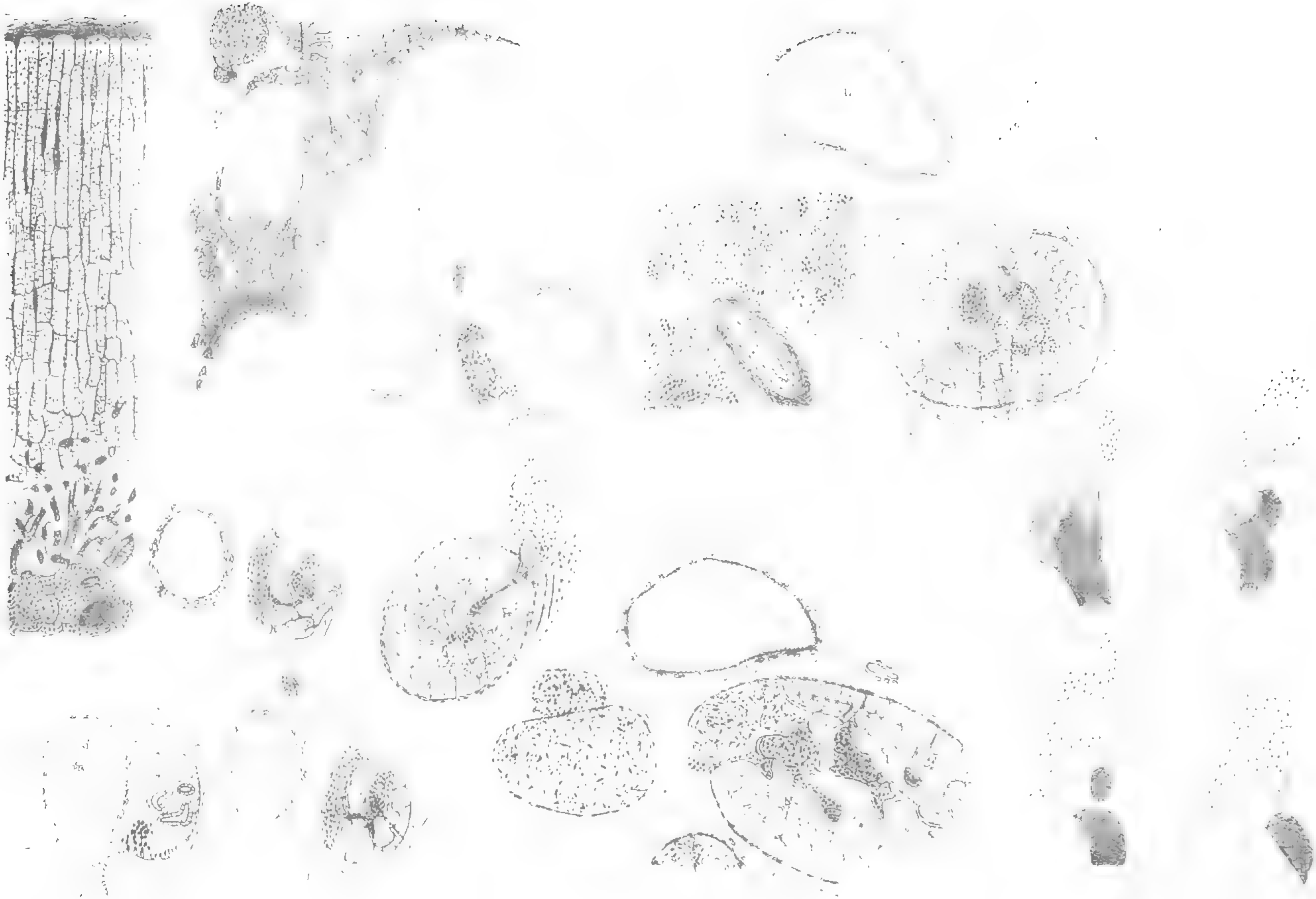


Fig. 8

Fig. 10

Pl. n, E I



On the DEVELOPMENT *of the* SUPRARENAL BODIES *in* MAMMALIA. By K. MITSUKURI, Ph.B., University of Tokio, Japan.

(With Plate VI.)

IT has for a long time been known that the suprarenal bodies are in close connection with the sympathetic system. As far back as 1839 Bergmann is said to have noted the fact. Remak, writing in 1847, clearly stated the relation on embryological grounds, and even went so far as to call the suprarenal bodies "Nervendrüsen." Leydig[1] is explicit in his statements in regard to the point. According to him, the suprarenal bodies in Selachians, Ganoids, and Reptiles, consist of two distinct parts. The one is enclosed, together with the usual ganglion cells, in successive sympathetic ganglia, and is made up of masses of cells different from the ganglion cells only in being dirty yellow in colour; the other part is derived from the former by the deposition of fat globules in the cells, and is situated on blood-vessels as yellowish masses. He further maintained that the ganglionic part corresponds to the medullary, and the yellowish masses to the cortical part of the Mammalian (and Avian ?) suprarenal bodies, which, in these classes, are coalesced into one mass on each side. According to this view the cortical part of the suprarenal bodies of the higher types must, therefore, be derived from the medullary—a conclusion which will be shown to be erroneous. It should be mentioned that in an earlier work[2] Leydig did not believe in the derivation of the one part from the other—in fact, considered the yellowish masses simply as collections of fat cells.

Balfour, in his 'Monograph on the Development of Elasmobranch Fishes,' mentions "two structures that have gone under the name of the suprarenal bodies." The one called by him the *interrenal body* is "an impaired rod-like body,

---

[1] 'Anatomisch-Histologisch Untersuchungen über Fische und Reptilien," Berlin; 1853, and 'Lehrbuch der Histologie des Menschen und der Thiere.'

[2] 'Beiträge zur Mikros. Anat. &c., der Rochen und Haie,' Leipzig, 1852.

lying between the dorsal aorta and the caudal vein, in the region of the posterior end of the kidneys." The other, named the *suprarenal bodies*, consists of "a series of paired bodies, situated dorsal to the cardinal veins on the branches of the aorta, and arranged segmentally." The former was believed by him to be developed from the mesoblast, and to have nothing to do with the latter, which are formed out of sympathetic ganglia, and remain in close connection with them throughout life. At that time Mr. Balfour was inclined to consider the *suprarenal bodies* homologous with the organ that goes under that name in the higher vertebrates, and the *interrenal* body, an altogether independent structure. He therefore agreed, to some extent, with the earlier view of Leydig. It will be seen that he has since modified his opinions.

Braun[1] studied the anatomy and development of the suprarenal bodies in Reptilians. In that class they are formed of two parts, viz. (1) masses of brown cells placed on the dorsal side of, and closely applied against, (2) irregular cords of cells, so full of oil globules that nuclei are altogether invisible in the fresh state. The first is derived from the sympathetic ganglia, and the second from the ordinary mesoblast. Here, clearly, the nervous cells, having the characteristic reaction of being stained brown by bichromate of potash, are homologous with the medullary, and the irregular cords containing oil globules, with the cortical part of the Mammalian suprarenals.

Brunn[2] makes an interesting statement in regard to the suprarenal bodies of birds. According to him the cells stained brown by bichromate of potash—*i. e.* the elements composing the medullary part of the mammalian suprarenals—are scattered throughout the organ between irregular cords of cells, which are like those composing the cortical part of the higher type.

Summing up these observations Mr. Balfour says, in his 'Comparative Embryology' (vol. ii, pp. 548-9), "The structure and development of what I have called the interrenal body in Elasmobranchii so closely correspond with that of the mesoblastic part of the suprarenal bodies of the Reptilia, that I have very little hesitation in regarding them as homologous; while the paired bodies in Elasmobranchii,

---

[1] M. Braun,—"Bau u. Entwick. d. Nebennieren bei Reptilien," 'Arbeit a. d. zool.-zoot. Institut, Würzburg,' vol. v, 1879.

[2] A. von Brunn.—"Ein Beitrag zur Kentniss des feineren Baues und Entwicklungsgeschichte der Nebennieren," 'Archiv für mikros. Anat.,' vol. viii, 1872.

derived from the sympathetic ganglia, clearly correspond with the part of the suprarenals of Reptilia, having a similar origin, although the anterior parts of the paired suprarenal bodies of Fishes have clearly become aborted in the higher types.

"In Elasmobranch Fishes we thus have (1) a series of paired bodies derived from the sympathetic ganglia, and (2) an unpaired body of mesoblastic origin. In the Amniota these two bodies unite to form the compound suprarenal bodies, the two constituents of which remain, however, distinct in their development. The mesoblastic constituent appears to form the cortical part of the adult suprarenal body, and the nervous constituent the medullary part."

In view of these considerations it seemed worth while to trace the development of the suprarenal bodies in Mammalia, and see whether the medullary part is actually derived from the sympathetic system and the cortical part from the mesoblast. Accordingly, at the instance of Mr. Balfour, I have been engaged in following the history of these bodies in the rabbit, and to some extent in the rat. The result has fully justified the conclusions set forth by Mr. Balfour in the above quotations. It will be shown in this article that the medullary part of the Mammalian suprarenals arise from the sympathetic nervous system, totally independently of and outside the mesoblastic cortical part, and becomes, in the course of development, transported into the middle of the cortical part, gaining only then the position which its name implies.

Before proceeding to describe the successive stages of development it may, however, be well to recall here briefly the essential points in the structure of the adult suprarenal bodies in Mammalia. The account given below will be understood to refer to the rabbit, unless otherwise specified.

Structure of the Adult Suprarenal Bodies.—In the rabbit the suprarenals lie, usually in a large quantity of fat, at some distance from the kidneys, near the opening of the renal vein into the vena cava inferior, and about on a level with the anterior end of the kidney of their respective side. The right is, therefore, somewhat in front of the left, and is, moreover, on the dorsal side of the vena cava, while the left is rather on the ventral side. The suprarenals themselves are oval, reniform, or elongated in shape, and lie with their longest diameter parallel with the axis of the body. The right suprarenal is often more elongated than the left, which is generally oval or reniform, in the latter case having its concave side turned towards the median line of the body. A large vein is seen to enter each suprarenal at its posterior end, which is a branch of the renal vein in the case of the left, and of the vena cava inferior in the right suprarenal. On cutting open a fresh suprarenal, in a median longitudinal plane, its division into whitish-yellow cortical part and greyish medullary part becomes at once obvious. The former exhibits also a subdivision into three more or less distinct layers. Starting from the outside, they are (1) a rather thin greyish layer; (2) yellowish layer comprising the main mass of the organ, and showing, even to the naked eye, radial striation; and (3) a layer, of a much darker yellow, adjoining to the medullary substance. These layers are for the most part arranged concentrically; but at the posterior end there is a modification in their relations, which, singularly enough, seems to have hitherto escaped observation. The medullary substance, instead of being covered by the cortical layers, as in other parts, here becomes attenuated into a narrow streak, and reaches the outside. Roughly speaking, therefore, the cortical substance is in the shape of a horseshoe, completely surrounding the medullary part, except at one point at the posterior end. The histological structure of this part is of great interest, as will be seen further on, on account of the peculiar developmental history of the medullary substance. A section of the suprarenal body across its shorter diameter will show three layers in concentric rings.

Fig. 1 shows a part of a transverse section of the suprarenal considerably magnified. If the whole section had been figured the outline would be oval, and the medullary substance (*m*), of which only a small portion is represented, would occupy a rather large irregularly oval area in the centre. In the figure, however, are shown all three parts of which the suprarenal is composed, viz. (1) the outer capsule of connective tissue (*d*), (2) the cortical substance (*a*, *b*, *c*), and (3) the medullary substance (*m*). I shall briefly describe each of these three portions.

Of the connective tissue capsules I need only say that nerves and blood-vessels are found embedded in it in tolerable abundance, and that bundles of connective-tissue fibres from the capsule are sent inwards to form the framework of the whole organ.

The whole space between the outer capsule and the medullary part is occupied by the cortical substance, which, therefore, constitutes the main mass of the organ. Briefly speaking, it is made up of large cells, supported in a very fine network of connective tissue—so fine that each cell has its own cavity in the mesh. These cells are collected into groups by coarser trabeculæ, and the forms these cell groups assume in different layers give characteristic appearances to any particular layer. We thus recognise in the suprarenals of the rabbit three distinct zones (*a, b, c,* fig. 1), which correspond to the three layers visible to the naked eye (see above). The outermost zone (*a*) shows cell groups in long radiating columnar rows, which, directly under the capsule, form small arches, as shown in the figure. The cells are more closely packed than in the middle zone. Between the columns are rather large, longish spaces (*w, w*), which are shown to be sections of blood-vessels by the endothelial cells lining them. This zone gradually passes into the inner (*b*), where the columns are shorter and thicker, and cells are not as closely packed. This zone forms, in most sections, by far the largest portion of the cortical substance. Its cells stand out beautifully Between the columns there may be seen, running radially, fine capillary blood-vessels, shown to be such by their endothelial cells. The innermost zone (*c*) has irregular cell groups, and is characterised by the presence of a great many blood-vessels (*v, v, v*). The latter, becoming larger and larger toward the centre by the union of numerous branches, finally open into the central large veins, found in the medullary substance, which, in their turn becoming one, leave the organ at its posterior end.

I may remark in passing that the two inner zones mentioned above correspond to the zona reticularis and zona fasciculata of Arnold,[1] but the outermost is different from his zona glomerulosa, as the cell groups are oval in the latter.

In sections cut with a freezing microtome from a fresh suprarenal, the whole cortical part is so filled with fat-like globules that it is hard to see anything else. These fat-like globules are not stained by osmic acid, and therefore do not seem to be true fat. In the process of hardening in picric and chromic acids and other reagents, except alcohol, they disappear completely. Even with specimens hardened in alcohol they seem to be lost in the process of embedding in wax.

The medullary cells are collected into oval or roundish groups by network of connective tissue, and I have not succeeded in seeing any one cell distinctly. The groups look like a collection of nuclei embedded in a mass of protoplasm. This alone would separate them from the cortical cells, each of which, as has been remarked, is placed in a special mesh

---

[1] 'Virchow's Archiv,' 1866.

of connective tissue, and stands out distinctly. There is, however, a reaction very characteristic of the medullary cells which is most useful in identifying them. When the suprarenals are hardened in bichromate of potash, the medullary substance is stained brown or yellow, and is sharply marked off from the cortical part. It occupies an area in the centre corresponding roughly to the outline of the section. The boundary between it and the cortical part is, however, most irregular, the latter sometimes going into the midst of the former, which, in its turn, may send long processes outwards. *In the last case we find almost invariably that the processes become continuous with nerve fibres, which frequently traverse the cortical substance from the capsule toward the medulla.*

Different authors have stated that the medullary part of various animals is very rich in ganglion cells. In the rabbit they are very scarce. Out of the numerous sections I have cut there is only one that shows undoubted nerve cells in the medulla. Large veins are found in this part (see fig. 1), and capillary spaces (*d*, fig. 2) are visible between cell groups.

Reference has been made to the posterior end of the suprarenal, where the medullary substance reaches the outside of the organ. By studying the consecutive sections of this part, we find the medullary cells following the vein to the posterior part, and finally, near the exit of the latter, emerging on the exterior. In the suprarenals of the fully-grown rabbit, the band of cells which follows the vein is rather narrow, while in those of young examples it is as wide as any part of the medullary substance. Fig. 2 is a longitudinal section of the posterior end of the suprarenal of an adult. The upper end of the figure is the posterior extremity of the suprarenal. The areas marked *c, c, c,* are occupied by cortical cells. If we follow the medullary substance (*m m*) a few sections towards the median plane of the suprarenal, we should find the point (*x*) gradually approaching the middle line of the section, and finally uniting with the main mass of the medullary substance in the centre of the organ. It will be seen in the figure that the medullary substance emerges at two points—on the top, and on the left side—and spreads itself over more or less wide areas on the surface of the suprarenal. At *f* it becomes continuous with irregular cords (*h*), made up of cell groups, which are exactly like those of the medulla, and some of which are stained yellow by bichromate of potash. They are, in fact, a part of the medulla. These cords (*h*) are continuous with the mass (*g*). This contains, in addition to small cells like those of the medullary substance, large, well-defined cells (*a*), with nuclei much larger than those of the surrounding cells. They seem to me to be nerve cells. In the sections of the corresponding part from a rabbit three weeks old I have seen an undoubted large ganglion on one side of the section, and I am almost certain that it becomes continuous with irregular cords, continuous in their turn with the medulla. In many places, as *b*, these cords taper and seem to pass off into fibres, which are certainly like nerve fibres, and at others, as *y*, nerves pass into cell masses, and are lost among them.

Taking these facts in connection with the developmental history of the medulla, it seems to me almost certain that the process of medullary substance emerging at the outer surface of the suprarenal at its posterior end becomes in some way intimately connected with nerves and ganglion cells. I may remark that Braun (loc. cit.) finds ganglia at the anterior and posterior terminations of the suprarenals in the Reptiles, and that the medullary cells are in intimate connection with them. My researches appear to show that the same arrangement obtains in the rabbit at the posterior end.

In the human suprarenals, according to 'Quain's Anatomy,' the arteries are derived from the aorta, the phrenic and the renal arteries. Brunn (loc. cit.) remarks that many arteries entering the connective-tissue capsule divide themselves in it into numerous fine branches; some of these go directly through the cortical substance to the medulla, but by far the majority form a close anastomosis in the capsule, and enter the suprarenal with larger process of connective tissue. The fine network of capillaries in the cortical and medullary part has already been mentioned. In regard to nerves, I am only certain of the existence of one in the rabbit arising from the sympathetic cords far in front in the dorsal region, and entering the suprarenal just within its posterior half. In 'Quain's Anatomy' nerves are stated to be derived from the solar plexus of the sympathetic and from the renal plexuses, and to be exceedingly numerous.

Development of the Suprarenal Bodies.—According to Kölliker,[1] the suprarenal bodies in the rabbit appear first on the twelfth or thirteenth day of gestation as masses of somewhat large round cells on each side of, and ventral to, the aorta, on the inner side of the Wolffian bodies, and dorsal to the mesentery.

---

[1] 'Entwicklungsgesch. des Menschen und der Höheren Thiere,' p. 954.

In one series of my sections of a twelve-day embryo several, that pass through what must become the front part of the future abdomen, show, at the spot designated by Kölliker, a mass of cells (*s.r.*, fig. 3) with large nuclei, stained with hæmatoxylin slightly darker than those of the surrounding cells. Dorsally this mass is tolerably distinctly separated off from other mesoblastic cells, but ventrally its termination is indefinite. This mass is probably the first rudiment of the mesoblastic or cortical part of a suprarenal body.

On the fourteenth day the suprarenals are already well marked. Fig. 4 shows the left suprarenal (*s. r.*) a few sections behind the front end. It consists of a mass of cell with large nuclei, divided into indefinite cords by blood capillaries which are already somewhat numerous. Cell limits are hardly visible. Mesoblastic cells surround the mass as a capsule. Dorsal to the suprarenal is placed another mass of cells (*n*) looking very much like the former, but if anything, with slightly smaller nuclei stained darker. This, on tracing it forward, is found continuous with the sympathetic cells (*symp.*, fig. 4), although at this stage the connection is not so obvious as later on.

The subsequent history shows that the medullary substance arises out of the above ventral mass (*n*) of the sympathetic system. From following the sections the suprarenal is found to be widest in the middle, and to taper both in front and behind. The cords of which it is composed are tolerably distinct, and the blood channels between them proportionally very wide and conspicuous. The sympathetic mass (*n*) gradually extends ventrally between the aorta and the suprarenal, and is continued back far beyond the posterior end of the suprarenal. It spreads, in some sections, around the latter, and in such cases it is difficult to tell the two bodies apart, as their structure at this early stage is very similar. It is only by tracing them back that they can be distinguished. The suprarenal and the sympathetic masses of the two sides remain, however, separate throughout.

In the suprarenals of sixteen-day embryos, great changes are observable. The medullary part (*m*, fig. 5) surrounded for the most part by the cortical substance (*c*) can now be clearly distinguished. In the medulla the nuclei of the cells are stained darker than in the surrounding part, and the medulla itself is at this stage nothing but a mass of simple cells with a mixture of a great number of spindle cells and other connective-tissue elements. The cortical substance is still made up of irregular cords of cells without any more definite structure. Closely applied against the suprarenal, on its inner side, there is a large mass of sympathetic nerve cells (*n*). At its ventral end, a process of this mass, partly composed of nerve fibres, enters the cortical substance at the point (*a*). The nervous mass has very much the appearance of the medullary substance—its nuclei being stained in the same way—although there are no connective-tissue cells visible in it. On tracing it forward it becomes continuous with the main sympathetic cord dorsal to the aorta. Fig. 6 shows a section immediately behind that represented in fig. 5. Here we see the branch (*a*, fig. 5) of the nervous mass (*n*) passing into the suprarenal and uniting with the medullary substance (*m*), a relation which affords strong presumptive evidence that the latter is derived from the nervous mass without. To demonstrate this point still more conclusively I have introduced here a figure (fig. 7) of a section of the suprarenal of an embryo rat about 23 millimètres long. In this figure there are to be seen nerve fibres (*b*) starting from the nervous mass (*n*) and entering the suprarenal (*s. r*). Amongst the fibres numerous cells (*m*), that look exactly like those in the mass (*n*),[1] have found their way into the middle of the suprarenal, and are clearly distinguishable from the surrounding cortical cells (*c*, *c*) as well by the structure of the cell groups as by their darker staining. In several sections, continuous with the one figured, strands of nerve fibres dividing from the main bundle may be seen proceeding into various parts of the suprarenal, and wherever they go, they are followed by nerve cells. That these cells become the medullary substance there can be no doubt, as I have seen the parts occupied by them stained brown by bichromate of potash in somewhat older rabbit embryos. I ought to add that the mass (*n*) is continuous with the main sympathetic cords.

As we trace the sections of the sixteen-day embryo rabbits backward, we find the nervous mass (*n*, figs. 5 and 6) gradually spreading towards the ventral side of the aorta, and there constituting what must be regarded as a sympathetic plexus. This plexus seems to join the medulla of the suprarenal at more than one point. The medullary substance continues to the posterior end of the suprarenal, occupying irregular areas more or less in the centre. Towards the posterior termination it occupies by far the larger portion of a section of the suprarenal, and is covered

---

[1] The engraver has unfortunately not represented the nuclei of the mass (*n*) very satisfactorily; so that their similarity with those of the medullary substance is not obvious.

by the cortical substance only on the outer side. The cortex finally disappears altogether, but the continuations of the medullary substance of the two suprarenals proceed backwards as paired cords along the ventral side of the aorta. These are evidently the "Geschlechtsnerven" of Remak, from the anterior part of which the suprarenals are stated by him to be developed. These cords join the continuation of the nervous mass (*n*, figs. 5 and 6) just at the point where the cortex ceases. The cords seem to unite with each other at one point, although soon separating again. Professor Kölliker (loc. cit. p. 953) remarks that in the sixteen- and seventeen-day embryo rabbits, the suprarenals of two sides unite behind, while the front parts are separate. It seems evident to me that he has not clearly distinguished between the cortical and medullary part. The cortical parts of two sides certainly show no signs of uniting with each other at any stage of development, while, if reference is made only to the continuations of the medullary part, it is not only in the sixteenth to seventeenth day, but at much later stages that they are found uniting with each other. Of certain histological peculiarities of other cords I shall speak later on.

The method of entrance of the medullary substance into the suprarenal bodies may be stated briefly as follows:—The peripheral sympathetic plexus, which is formed ventrally to the aorta in the abdominal region, sends in processes into the body of suprarenals at various points—the one at the posterior end of the organ being by far the largest—and the cells thus carried in become gradually transformed into the cells of the medullary substance.

In embryos of sixteen days, all the essential parts of the suprarenals are already present, and henceforth the development consists simply in their histological elaboration:—I shall rapidly describe the successive stages until we come to the twenty-sixth day, which, being the last I have observed, I shall treat of somewhat minutely. On the eighteenth day the suprarenals are already visible to the naked eye as oval bodies on the inner side of the kidney, and substantially resemble the adult bodies in regard to position, shape, and symmetry. This stage is the earliest of which I have embryos hardened in bichromate of potash.

The medullary part takes already a slight brown staining, and it is to be specially noted that the continuation of it behind the cortical substance is also affected in the same way. The cortical substance has increased considerably in quantity, and the irregular cords of cells begin to assume a more regular oval or polygonal form. In regard to the embryos of the twentieth, twenty-second, and twenty-fourth days, of which I have sections, there is nothing special to mention, except that the suprarenals become gradually larger, that the medullary and cortical substances increase accordingly, and that the cell groups in the cortex become more and more definite and the trabeculæ between them finer. We now come to the twenty-six-day embryos. Fig. 8 shows a transverse section of the left suprarenal (*s. r.*) about in the middle of the organ. The cortex (*c, c*) is already made up of definite cell groups, although not yet divided into the different zones found in the adult. The connective-tissue framework is now so fine that each cell has its own special mesh, although not so represented in the figure. Capillaries between the cell groups are well formed. The differentiated medullary substance is not so far advanced as that of the cortical part; it is divided into irregular groups of cells, whose nuclei are stained darker than those of the cortex. Its veins (*v, v*) are very conspicuous. The connective-tissue capsule is well developed.

The sympathetic nervous masses (*n, n*) are now full of distinct ganglion cells, supported in a connective-tissue network. Scattered among the larger cells are smaller cells, as at *a*. Fig. 9 shows a section of the same suprarenal near its posterior end. It will be seen that the cortex (*c, c*) no longer completely surrounds the medullary part, but is open toward the inner side. If we trace it backward we shall find it occupying less and less space in the section of the suprarenal, and gradually confining itself to the outer side. Finally, having greatly diminished in quantity, it separates from the medullary part, and soon after ends on the ventral side of the vena cava inferior. The diagrammatic longitudinal section of the same part, shown in fig. 10 A, will make the relations clear. The cortical substance (*c*) is present only on the ventral side at the posterior end of the suprarenal; and, if it were possible to show this in the same figure, would be also visible on the outside; while the medullary substance (*m.*) is confined to the dorsal and inner region. Certain parts of the medullary substance present very peculiar features. I refer to the parts marked *p, p* in fig. 9. In them, spindle and stellate connective-tissue cells are very abundant, and, by the union of their processes, seem to divide the whole space into irregularly polygonal areas. In these areas there are placed a number of small cells, somewhat like those of the central part of the medullary subtance, with which the part *p, p* is directly continuous. It is the part of the medullary substance (*p*, *p*) which is continued posteriorly beyond the end of the suprarenal, as paired cords on the ventral side of the aorta. In fact, the part marked *p* on the left side of fig. 9 is continued from the right suprarenal, which has ended several sections in front. That this structure is really a part of the medullary substance there can be no question, as it is stained brown by bichromate of potash. It extends backwards much more than the length of the suprarenals themselves. For instance, in an embryo of twenty-four days, the right suprarenal appears in about forty sections, and the left in about thirty, while these cords extend posteriorly for about fifty-five sections from the termination of the left suprarenal. The cords unite with each other several times, soon, however, separating again. Posteriorly, they gradually lose their brown colour, and seem then made up of nerve fibres. Nerves may also join them, where they still exhibit the typical brown reaction. It is probable, from the comparison of the sections of embryos hardened in picric acid and potassium bichromate, that so long as the histological structure shown in *p*, fig. 9, is observable, the cords are stained brown. I have carefully traced the cords forward both in the longitudinal and transverse sections, and find that they become continuous with the nervous mass (*n*) shown in fig. 8. This is obvious from the series of sections in fig. 10. A is the outermost, the sections gradually going towards the median axis of the body of the embryo. In A the cortex (*c*) is quite large, while the part marked *p* (same as *p*, fig. 9) is continuous with the medullary substance (*m*). The nervous mass (*n*, of fig. 8) is here also marked *n*. In B the cortex (*c*) is disappearing; in C it has completely disappeared, and the part marked *p* has divided into two parts (*p* and *a*). Lastly, in D, we see that the nervous mass (*n*) has united with the small mass marked *a* in C. Thus there can be no doubt that the structure *p*, figs. 9 and 10, is continuous with the nervous mass *n*, fig. 8, and must be of a nervous nature. And yet it has not a single typical ganglion cell, and there is a considerable difference between its microscopic appearance and that of the nervous mass (*n*, figs. 8, 9, and 10). It is possible that the cells that are found in *p* are of the same nature as the smaller cells in the nervous mass. The only conclusion that I can arrive at is that this part of the peripheral sympathetic system becomes early distinguished from the other parts by an enormous development of connective-tissue cells, and by a total absence of ganglion cells, and that all this is preparatory to its transformation into the medullary substance of the suprarenal. The irregular polygonal areas, in which the cells are embedded, are not unlike the cell groups of the medullary substance, and might be easily transformed into them. This, taken in connection with the facts that this structure (*p, p,* figs. 9 and 10) is directly continuous with the medullary substance, and seems gradually to pass into it, and that it is stained by bichromate of potash seems to justify this conclusion. Its posterior extension presents no objection to this view, as we have seen that in the adult suprarenal the medullary substance is found outside the organ in a corresponding region.

The results at which I have arrived in the preceding pages may be summed up as follows:

(1) The suprarenal bodies in Mammalia are composed of two parts—the cortical and the medullary—totally different in their origin.

(2) The cortical substance arises from the mesoblast.

(3) The medullary substance is derived from the peripheral part of the sympathetic system, and is at first placed outside of the cortical substance, becoming transported into the middle of the suprarenal body in the course of development.

I may also call attention once more to the interesting gradation of the structure of the suprarenals in different groups of Vertebrata. In Elasmobranchs the two components of the suprarenals are totally independent of each other. The sympathetic part is found in successive sympathetic ganglia, while the mesoblastic part is a median unpaired body. In Reptilia the sympathetic part is no longer bound up in sympathetic ganglia, but is closely applied against the dorsal side of the mesoblastic part, which is paired. In Aves the sympathetic part has found its way inside of the mesoblastic part, but is as yet irregularly scattered throughout the organ (Brunn). Finally, in Mammalia the sympathetic part is collected into one mass, and occupies an area in the centre of the mesoblastic part, although still showing its origin in its development.

In conclusion, I wish to express my sincerest obligations to Mr. Balfour, with whom the idea of the present investigation originated, for his uniform kindness in giving me his valuable advice, and also for the facilities which he has afforded me in his laboratory for pursuing my work.

On the STRUCTURE *and* DEVELOPMENT *of* LEPIDOSTEUS.

By F. M. BALFOUR, LL.D., F.R.S., and W. N. PARKER.[1]

THE authors commence this paper by thanking Professor Alexander Agassiz for the material, both embryological and adult, on which these researches were made.

The first section is devoted to the general development. In this section an account is given of the structure of the ripe ovum, of the segmentation, of the history of the germinal layers, of the first development of the principal organs, and of the external features of the embryo during embryonic and larval life. The more important points established in this section are—

(1.) The ovum when laid is invested by a double covering formed of (*a*) a thick inner membrane, the outer zone of which is radially striated, and (*b*) an outer layer made up of highly refractive pyriform bodies which are probably metamorphosed follicular epithelial cells.

(2.) The segmentation is complete, though very unequal; the lower pole being very slightly divided into segments, and its constituent parts subsequently fusing together to form an unsegmented mass of yolk, like the yolk-mass of Teleostei.

(3.) The epiblast is divided into an epidermic and a nervous stratum, as in Teleostei.

(4.) The walls of the brain, of the spinal cord, and of the optic vesicles are formed from a solid medullary keel, like that found in Teleostei.

(5.) The lens, the auditory vesicle, and the olfactory pit, are wholly developed from the nervous layer of the epidermis.

(6.) The segmental or archinephric duct is developed, as in Teleostei, from a hollow ridge of the somatic mesoblast, which becomes constricted off, except in front; thus forming a duct with an anterior pore leading into the body cavity.

The section on the general development is followed by a

---

[1] This paper is an abstract of one which will be published in full in the 'Philosophical Transactions of the Royal Society.'

series of sections on the adult anatomy and development of various organs.

The Brain.—The authors give a fuller description of the adult brain than previous anatomists. The new features in this description are (1) that the parts identified by previous anatomists as the olfactory lobes, are really parts of the cerebral hemispheres; the true olfactory lobes being small prominences at the base of the olfactory nerves; (2) that there is attached to the roof of the thalamencephalon a peculiar vesicle, which has not hitherto been noticed, but which is similar to the vesicle found by Wiedersheim on the roof of the thalamencephalon of Protopterus. They further show that the cerebrum is divided into a posterior portion, with an unpaired ventricle, and an anterior portion in which the ventricle is paired. They consider the presence of a portion of the cerebrum with an unpaired ventricle to be an indication that this part of the brain retain characters which are only found in the embryonic brain of other groups. They point to the presence of lobi inferiores on the infundibulum, of tori semicirculares in the mid-brain, and of a large cerebellum as indications of an affinity between the brain of Lepidosteus and that of Teleostei. In the embryological section full details are given as to the development of the thalamencephalon, the pineal gland, the cerebrum, and the olfactory lobes.

At the end of the section the characters and affinities of the Ganoid brain are dealt with at some length; and the authors attempt to show that brains of Ganoids are distinguished (1) by the large size of the thalamencephalon, and (2) by the cerebrum being divided into an unpaired portion behind and a paired portion in front.

Organs of Special Sense—*Olfactory Sacs.*—An account is given of the development of the olfactory sacs, in which these sacs are shown to originate as invaginations of the nervous layer of the epiblast; the communication between the sacs and the exterior being effected by the rupture or absorption of the superficial epidermic layer of the epiblast. The double opening of these sacs in the adult is described as arising from the division of the primitive single opening. The olfactory nerve arises as an outgrowth of the brain prior to the first differentiation of the olfactory bulb as a special lobe of the brain.

Eye.—In the adult eye a vascular membrane is described bounding the retinal aspect of the vitreous humour. This membrane is supplied by an artery piercing the retina close to the optic nerve, and the veins from it fall into a circular vessel placed at the insertion of the iris. The membrane itself is composed of a hyaline ground substance with numerous nuclei.

In the developmental section devoted to the eye the main subject dealt with is the nature of the mesoblastic structures entering the cavity of the optic cup through the choroid slit. It is shown that a large non-vascular mesoblastic process first enters the optic cup, and that together with the folded edge of the choroid slit it forms a rudimentary and provisional *processus falciformis.* At a later period an artery, bound up in the same sheath as the optic nerve, enters the optic cup, and the vascular membrane found in the adult then becomes developed.

The Suctorial Disc.—The structure of a peculiar larval suctorial organ, placed at the end of the snout, is described, and the organ is shown to be formed of papillæ composed of elongated epidermic cells, which are probably glandular (modified mucous cells), and pour out a viscid secretion.

Muscular System.—The lateral muscles of Lepidosteus are shown to differ from those of other fishes, except the Cyclostomata, in *not* being divided into a dorso-lateral and ventro-lateral group, on each side of the body.

Vertebral Column and Ribs.—This section of the paper commences with a description of the vertebral column and ribs of the adult. In this part special attention is called to a series of cartilaginous elements, placed immediately below the ligamentum longitudinale superius, which appear to have escaped the notice of the anatomists who have previously worked at Lepidosteus. These elements are shown to be intervertebrally situated.

With reference to the ribs the authors point out that for the greater part of their length they course along the bases of the intermuscular septa, immediately external to the peritoneal membrane, but that their free extremities bend outwards and penetrate between the muscles along the intermuscular septa till they nearly reach the skin.

In the embryological part of this section a detailed account is given of the development of the vertebral column, of which the following is a summary:

There is early formed round the notochord a mesoblastic investment which is produced into two dorsal and two ventral ridges, the former uniting above the spinal cord. Around the cuticular sheath of the notochord an elastic membrane, the membrana elastica externa, is next developed. The neural ridges become enlarged at each intermuscular septum, and these enlargements soon become converted into cartilage, thus forming a series of neural processes, riding on the membrana elastica externa, and extending about two thirds of the way up the sides of the spinal cord. Hæmal processes arise simultaneously with and in the same manner as the neural; they are small in the trunk, but at the front end of the anal fin they suddenly enlarge and extend ventralwards. Behind this point each succeeding pair of hæmal processes becomes larger than the one in front, each process finally meeting its fellow below the caudal vein, thus forming a completely closed hæmal arch. These arches are, moreover, produced into long spines supporting the fin-rays of the caudal fin, which thus differs from the other unpaired fins in being supported by parts of the vertebral column, and not by separately formed skeletal elements.

In the next stage which the authors have had the opportunity of studying (a larva of 5½ centims.), a series of well-marked *vertebral* constrictions are to be seen in the notochord. The sheath is now much thicker in the vertebral than in the intervertebral regions; this being due to a special differentiation of a superficial part of the sheath, which appears more granular than the remainder, and forms a cylinder in each vertebral region. Between it and the gelatinous tissue of the notochord there remains a thin unmodified portion of the sheath, which is continuous with the intervertebral parts of the sheath. The neural and hæmal arches, which are of course placed in the vertebral regions, are now continuous with a cartilaginous tube embracing the intervertebral regions of the notochord, and continuous from one vertebra to the next. A delicate layer of bone, developed in the perichondium, invests the cartilaginous neural arches, and this bone grows upwards so as to unite above with the osseous investment of separately developed bars of cartilage, which are directed obliquely backwards. These bars, or dorsal processes, may be reckoned as parts of the neural arches. Between the dorsal processes of the two sides are placed median rods of cartilage, which are developed separately from the true neural arches, and which constitute the median spinous elements of the adult. Immediately below these rods is placed the ligamentum longitudinale superius. There is now the commencement, not only in the tail but also in the trunk, of a separation between the dorsal and ventral parts of the hæmal arches where the latter pass ventralwards, on each side of the body cavity, along the lines of insertion of the intermuscular septa. They are obviously the ribs of the adult, and there is no break of continuity of structure between the hæmal arches of the tail and the ribs. In the anterior part of the trunk, the ribs pass outwards along the intermuscular septa till they reach the epidermis. Thus the ribs are originally continuous with the hæmal processes. Behind the region of the ventral caudal fin the two hæmal processes merge into one, which is not perforated by a canal.

Each of the intervertebral rings of cartilage becomes eventually divided into two parts, which are converted into the adjacent faces of contiguous vertebræ, the curved line where this will be effected being plainly marked out at a very early stage. As these rings are formed originally by the spreading of the cartilage from the primitive neural and hæmal processes, the intervertebral cartilages are clearly derived from the neural and hæmal arches. The intervertebral cartilages are thicker in the middle line than at their two ends.

In the latest stage examined (11 centims. long) the vertebral constrictions of the notochord are rendered much less conspicuous by the intervertebral cartilages giving rise to marked intervertebral constrictions. In the intervertebral regions the membrana elastica externa has become aborted at the posterior border of each vertebra, and the remaining part is considerably puckered transversely. The inner sheath of the notochord is puckered longitudinally in the intervertebral regions. The granular external layer of the sheath in the vertebral regions is less thick than in the last stage, and exhibits a faint radial striation.

Two closely approximated cartilaginous elements now form a key-stone at each neural arch above; these are directly differentiated from the ligamentum longitudinale superius, into which they merge above. An osseous plate is formed on the outer side of each of these cartilages. These plates are continuous with the lateral osseous bars of the neural arches, and give rise to the osseous part of the roof of the spinal canal of the adult. Thus the greater part of the neural arches is formed by membrane bone.

The hæmal arches are invested by a thick layer of bone, and there is also a continuous osseous investment round the vertebral portions of the notochord. The intervertebral cartilages become penetrated by branched processes of bone.

The embryological part of this section is followed by a comparative part treated under three headings. In the first of these the vertebral column of Lepidosteus is compared with that of other forms; and it is pointed out that there are grave difficulties in the way of comparing the vertebræ of Lepidosteus with those of the Urodela, in the fact that in Lepidosteus the intervertebral cartilages originate from the bases of the arches, while in the Urodela they are stated by Götte to be thickenings of a special cartilaginous investment of the notochord, which would seem to be homologous with that cartilaginous sheath which is placed in Elasmobranchii and Dipnoi *within* the membrana elastica externa. On the other hand, the development of the vertebræ of Lepidosteus is shown to resemble in most features that of Teleostei, from which it mainly differs in the presence of intervertebral cartilaginous rings.

In the second section, devoted to the homologies of the ribs of Pisces, the conclusions arrived at are summed up as follows:

The results of the authors' researches appear to leave two alternatives as to the ribs of fishes. One of these, which may be called Göttes view, may be thus stated:—The hæmal arches are homologous throughout the Pisces; in Teleostei, Ganoidei and Dipnoi, the ribs, placed on the inner face of the body wall, are serially homologous with the ventral parts of the hæmal arches of the tail; in Elasmobranchii, on the other hand, the ribs are neither serially homologous with the hæmal arches of the tail, nor homologous with the ribs of Teleostei and Ganoidei, but are outgrowths of the hæmal processes into the space between the dorso-lateral and ventro-lateral muscles, and outgrowths which may perhaps have their homologies in Teleostei and Ganoids in certain accessory processes of the vertebræ.

The other view, which the authors are inclined to adopt, is as follows:—The Teleostei, Ganoidei, Dipnoi and Elasmobranchii are provided with homologous hæmal arches, which are formed by the coalescence below the caudal vein of simple prolongations of the primitive hæmal processes of the embryo. The canal enclosed by the hæmal arches can be demonstrated embryologically to be the aborted body cavity.

In the region of the trunk the hæmal processes and their prolongations behave somewhat differently in the different types. In Ganoids and Dipnoi, in which the most primitive arrangement is probably retained, the ribs are attached to the hæmal processes, and are placed immediately without the peritoneal membrane, at the insertion of the intermuscular septa. These ribs are in many instances (Lepidosteus, Acipenser), and very probably in all, developed continuously with the hæmal processes, and become subsequently segmented from them. They are serially homologous with the ventral parts of the hæmal arches of the tail, which, like them, are in many instances (Ceratodus, Lepidosteus, Polypterus, and to some extent in Amia) segmented off from the basal parts of the hæmal arches.

In Teleostei the ribs have the same position and relations as those in Ganoids and Dipnoi, but their serial homology with the ventral parts of the hæmal processes of the tail is often (*e.g.* the Salmon) obscured by the anterior hæmal arches (*i.e.* those in the posterior part of the trunk) being completed, not by the ribs, but by independent outgrowths of the basal parts of the hæmal processes.

In Elasmobranchii a still further divergence from the primitive arrangement is present. The ribs appear to have passed outwards, along the intermuscular septa, into the muscles; and are placed between the dorso-lateral and ventro-lateral muscles (a change of position of the ribs of the same nature is observable in Lepidosteus). This change of position, combined probably with the secondary formation of a certain number of anterior hæmal arches, similar to those in the Salmon, renders their serial homology with the ventral parts of the hæmal processes of the tail far less clear than in other types; and further proof is required before such homology can be considered as definitely established.

Under the third heading the skeletal elements supporting the fin-rays of the ventral lobe of the caudal fin of various types of fishes are compared, and the following conclusions are arrived at:

(1.) The ventral lobe of the tail-fin of Pisces differs from the other unpaired fins in the fact that its fin-rays are directly supported by spinous processes of certain of the hæmal arches, instead of by indently developed interspinous bones.

(2.) The presence or absence in the tail-fin of fin-rays, supported by hæmal arches, may be used in deciding whether apparently diphycercal tail-fins are aborted or primitive.

Urogenital Organs.—With reference to the character of the adult urogenital organs, the authors show that for the female the descriptions of Müller and Hyrtl are substantially accurate, but that Hyrtl's description of the generative ducts of the male is wholly incorrect.

They find that in the male the semen is transported from the testes by means of a series (40—50) of vasa efferentia, supported by the mesorchium. In the neighbourhood of the kidney these vasa unite into a longitudinal canal, from which transverse trunks are given off, which become continuous with the uriniferous tubuli. The semen is thus transported through the kidney into the kidney-duct (segmental duct), and so to the exterior. No trace of a duct homologous with the oviduct of the female was found in the male.

With reference to the development of the excretory system, the authors have established the following points :

(1.) That the segmental (archinephric) duct is developed as in Teleostei.

(2.) That a pronephros, resembling in the main that of Teleostei, is developed from the anterior end of the segmental duct. But they find that the pronephric chambers, each containing a glomerulus, into which the coiled pronephric tubes open, are not, as in Teleostei, completely shut off from the body cavity, but remain in communication with it by two richly ciliated canals, one on each side of the body.

(3.) The pronephros eventually undergoes atrophy.

(4.) Some of the mesonephric tubes have peritoneal funnels in the larva.

(5.) The ovarian sac continuous with the oviduct is established by a fold of the peritoneal membrane, near the attachment of the mesovarium, uniting with the free edge of the ovarian ridge to form a canal, the inner wall of which is constituted by the ovarian ridge itself.

(6.) The posterior part of the oviduct is not formed until the ovarian sac has become developed, and had not been developed in the oldest larva (11 centims.) the authors have succeeded in obtaining.

The Alimentary Canal and its Appendages.—In this section the authors give a detailed account of the topographical anatomy of the alimentary tract in the adult. They have detected a small pancreas close to the bile-duct, and call special attention to a ventral mesentery passing from the posterior straight section of the intestine to the ventral wall of the body.

In the embryological part of the section a detailed account is given of the development (1) of the pancreas, which is described as arising as a dorsal diverticulum of the duodenum on a level with the opening of the bile-duct; (2) of the yolk sac and vitelline duct; (3) of the spiral valve, which first appears as a hollow fold in the wall of the intestine, taking a slightly spiral course, and eventually becoming converted into a simple spiral ridge.

The so-called hyoid gill, which the authors expected to find well developed in the larva, is shown not to be found even in the oldest larva the head of which was examined (26 mm.).

The last section of the paper is devoted to the consideration of the systematic position of Lepidosteus. The Teleostean affinities of Lepidosteus are brought into prominence, but it is shown that Lepidosteus is nevertheless a true Ganoid.

The arguments used in this portion of the paper do not admit of being summarised.

On CERTAIN POINTS *in the* ANATOMY *of* CHITON. By ADAM SEDGWICK, M.A., Fellow of Trinity College, Cambridge.

An account of the structure of the kidney of Chiton has long been a want in morphology. Middendorff,[1] in 1848, described a branched gland lying ventrally on each side of the body cavity which he identified as kidney; but he records no observation on the structure of the gland, and expressly states that he was not able to make out its opening or relation to other organs. Schiff,[2] ten years later, was unable to find this gland in *Chiton piceus*, and throws doubt on Middendorff's interpretation of its function.

Von Jhering[3] has comparatively recently recorded some observations on the kidney of Chiton, and starts from the position that no kidney is known in Chiton, Middendorff's view as to the nature of the branched gland having been sufficiently refuted by Schiff's later observations. Von Jhering states that in the species of Chiton observed by him the kidney consists of a branched gland lying ventral to the rectum in the hinder part of the body cavity, and that it opens by a single median pore ventral to the anus. He further figures this opening.

While staying at Herm this summer I found a fair number of a good-sized species of Chiton—*Chiton discrepans;* and the results which I have obtained from the study of the anatomy of this form, especially those which concern the kidney, seem to me sufficiently important for immediate publication. In the first place, I may mention that I have seen nothing in any of my dissections or sections which in the least supports von Jhering's statements as to the existence of a median renal duct and opening; and that my observations are entirely opposed to the conclusion arrived at by this investigator as to the unpaired nature of the kidney of Chiton. On the contrary, Middendorff's observa-

---

[1] 'Mémoires de l'Acad. de St. Pétersbourg,' 6th ser., vol. vi.

[2] Schiff, 'Zeit. f. Wiss. Zool.,' Bd. ix.

[3] 'Morphol. Jahrbuch,' Bd. iv.

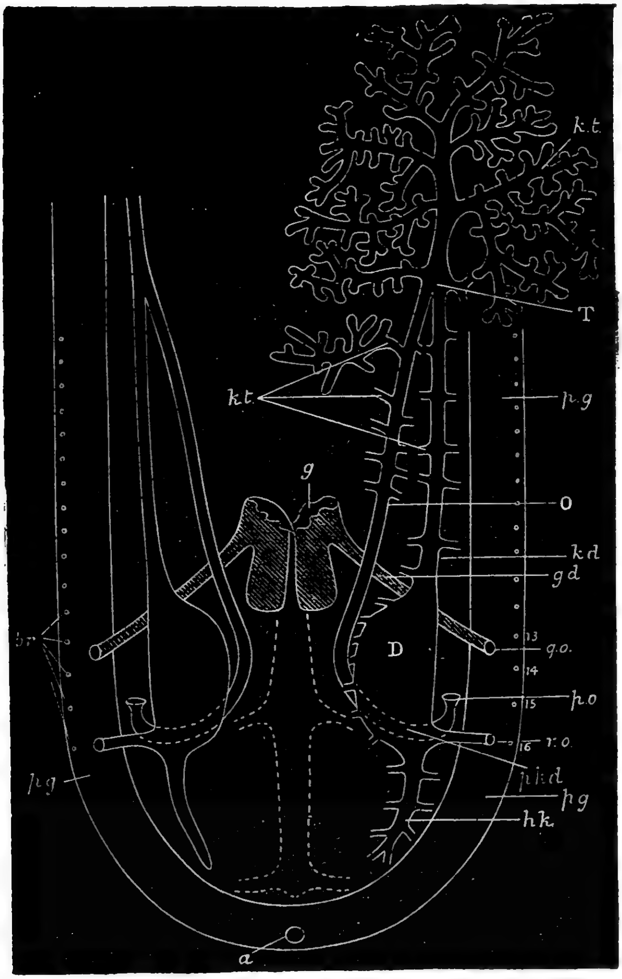
tions, so far as they went, were perfectly correct. The paired lateral-branched gland described by the latter observer is part of the kidney.

The kidney of Chiton is a paired gland with paired openings into the pallial groove and into the pericardium, and is constructed on the type always found in molluscan renal organs (fig. 1). It opens in the species I have chiefly examined (*Chiton discrepans*) into the pallial groove (fig. 1, *r.o.*) internal to, but on a level with the last gill (16). The duct runs from the opening round the outside border of the pallial nerve (fig. 2, *r.o.*), and then passes inwards to open into a bladder-like structure placed in the body cavity (fig. 1, D, and fig. 2, D). This bladder-like structure lies close to the body wall immediately beneath the pericardium (fig. 2, *p.c.*), and it does not seem to extend backwards beyond the last gill.

On a closer examination by means of sections, it is seen to be beset by a number of branched glandular cæca, lying in the hinder part of the body cavity (fig. 2, *k.t.*), which open into it, and into a backward prolongation from it (fig. 1, *h.k.*). These branched glandular cæca on opening the body cavity are seen as a mass of tubes apparently interlacing with those of the opposite side, and lying ventral to the rectum on the floor of the body cavity (fig. 2, *k.t.*). This portion of the kidney has been seen and described by von Jhering, but instead of constituting the whole of the kidney and opening to the exterior by a median pore, it is only the posterior part, and opens on each side into the bladder-like structure which opens to the exterior in the position described above. I have many series of sections through this hinder part of the kidney of Chiton, which prove most conclusively that these hinder ventrally-placed tubules do open in the way I have stated.

On examining the anterior end of the bladder-like structure it is found that it is continued forwards as a duct (fig. 1, *k.d.*), which receives, all along its course, the ducts of bunches of branching glandular cæca, lying at the side of the body cavity (fig. 1, *k.t.*). These branching glandular cæca constitute the gland described by Middendorff. Their structure precisely resembles that of the first described posterior tubules, which open into the dilated part of the duct and its backward prolongation. The duct can be traced forward to about the level of the fourth shell-plate (fig. 1, T), at which point it turns sharply round and runs back parallel with the first part of its course. A considerable part of the gland lies in front of this turning point of the duct; the secretion

FIG. 1.

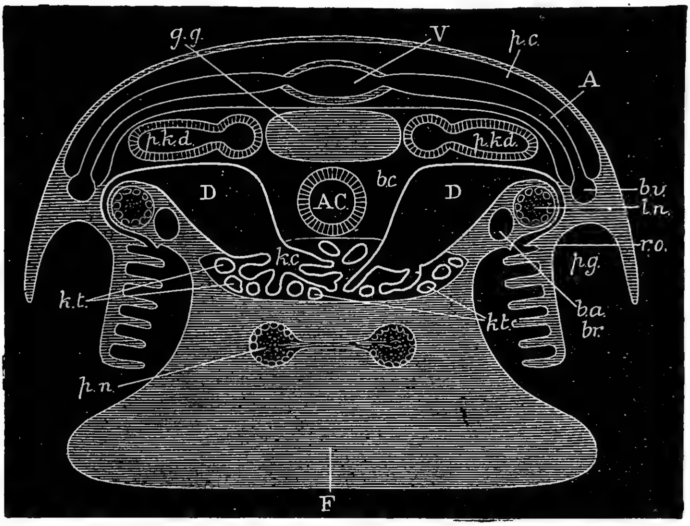


A diagrammatic representation of the kidney and generative ducts of *Chiton discrepans*, viewed from the ventral surface. The pallial groove is represented as enclosed by the lines *p.g.*; and in it are seen the 16 gills (*br.*), the generative (*g.o.*) and renal (*r.o.*) orifices; and the anus (*a.*). The branched nature of the kidney is shown in the anterior part of the figure on the right side; posteriorly these secreting tubules are omitted. On the left side of the figure the kidney duct alone is indicated.

a., anus; *br.*, branchiæ; D, dilated part of kidney duct opening to exterior; *g.* points to the junction of the generative duct with the generative gland; the generative gland is supposed to be torn away; *g.d.*, generative duct; *h.k.*, posterior part of kidney duct; *g.o.*, generative orifice; *k.t.*, secreting tubules of kidney; *k.d.*, duct of kidney running forward, bending round at T and running back, receiving glands as far back as O. From O it runs to the pericardial opening *p o.*, receiving no glands; *p.g.*, pallial groove; 13, 14, 15, 16, last four branchiæ; the ventricle and auricular openings are indicated by dotted lines.

of this part is poured into a branch given off from the main duct at the bend (fig. 1, T). The posteriorly directed part of the renal duct lies close to the dorsal edge of the part running forward, and, like the latter, receives the efferent ducts of bunches of glandular cæca (fig. 1). From the level of the fifth shell-plate (fig. 1, O) to its posterior termination (fig. 1, *p.o.*), about to be described, it receives no glandular

Fig. 2.



A diagrammatic representation of a transverse section through *Chiton discrepans* at the level of the renal orifices (*r.o.*, fig. 1). Dorsally is the pericardial cavity with the heart, separated by the pericardial floor from the general body cavity (*b.c.*), containing the viscera. Ventrally is the posterior apparently median unpaired part of the kidney (*k.t.* and *k.c.*) seen by von Jhering. A little in front of this section the kidney tubules take up a distinctly lateral position.

D; *p.g.*; *b.r.*; *k.t.*; *r.o.* as in fig. 1.

A, auricle; V, ventricle; *b.v.*, branchial vein; *b.a.*, branchial artery; *p.c.*, pericardial cavity; *l.n.*, lateral nerve (pallial); *p.n.*, pedal nerve; F, foot; A.C., alimentary canal; *g.g.*, generative gland; *b.c.*, body cavity; *k.c.* see *k.t.*; *p.k.d.*, part of kidney duct which in fig. 1 is hidden from view by D.

cæca, but runs backwards as a simple duct distinguishable by its brown colour, which is due to a deposit of colouring matter in its walls. On reaching the level of the bladder-like dilatation of the kidney duct first described, it applies itself to the dorsal inner wall of that structure as far back as the level of the last gill. At this point, which marks the hind border and the external opening of the bladder, it runs outwards and then forwards (fig. 2, *p.k.d.*) in close contact with the dorsal side of the lateral nerve cord. It runs forward to about the level of the penultimate gill, where it suddenly stops and opens by a small pore into the pericardium (fig. 1, *p.o.*) beneath, *i.e.* ventral to the anterior part of the auricle.

Comparing the arrangement of the kidney of Chiton with that of Anodon, there is seen to be a close agreement. In both the kidney is paired and consists of a gland bent on itself, opening at the one extremity into the pallial cavity, and at the other into the pericardium. In both the kidney is unsegmented (a fact to be remembered when the nature of the shell and gills of Chiton is discussed). There is a further agreement between these two animals in the relation of the openings of the generative ducts to those of the renal ducts; in both the latter are placed close behind the former.

With regard to the minute structure of the kidney of Chiton I have no exact observations. It is necessary to study it in the fresh state. The inner borders of the cells lining the glandular cæca are stated by von Jhering to be ciliated.

The most internal part of the kidney duct, *i.e.* that which receives no glandular cæca (fig. 1, O to *p.k.d.*), is, with the exception of a small portion adjoining the pericardial opening, lined by columnar cells containing a yellow colouring matter, which gives this portion of the duct a yellow colour, easily visible to the naked eye. This yellow colouring matter, which seems to be part of the excretion of the cells lining the duct, is absent in the part of the duct which runs forwards from the level of the hinder edge of the bladder to the pericardial opening (*p.k.d.* to *p.o.*). Here are found large columnar cells provided with long cilia, which line also the pericardial opening.

The cells of the glandular cæca seem to have the structure usually seen in molluscan renal organs, and have been correctly described by von Jhering.

To sum up, the kidney of Chiton consists of—

(1.) A duct opening to the exterior in the pallial groove behind the generative opening, and internally into the pericardium.

(2.) Glandular cæca opening into this duct.

The duct may be described as consisting of three parts:

(1.) The part into which the glandular cæca of the kidney open. This part is open behind where it opens to the exterior (fig. 1, D). In front it bends round (fig. 1, T), and runs backward to about the level of the fifth shell plate, where it changes its character, and is continuous with (2) a duct (fig. 1, O) containing brown colouring matter in the columnar cells lining it, and receiving no glandular cæca. This part extends back to the level of the last gill, where it turns outwards, and becomes continuous with (3) a part running forward for a short distance close to the lateral nerve, and lined by large ciliated columnar cells. This part opens in front at the level of the penultimate gill into the pericardium (fig. 1, *p.o.*). I expected to find the communication between the two parts of the renal duct behind in the region of the bladder, and for some time I was puzzled at not finding it. On mentioning the arrangement of parts to Mr. Balfour, he suggested that the communication might possibly be found in front, reasoning from the analogy of the structure of the kidney in other Mollusca. On examining the anterior part of the gland more carefully, I at once found that his suggestion was correct, the two parts of the gland communicating as I have described. I have no observations to add to those of previous observers, on the general arrangement of the nervous system. I may mention that the lateral and pedal nerves have a coating of ganglion cells and a central core of fibres.

The animals are diœcious. The generative gland is unpaired and dorsal. The generative ducts are paired, and are attached to the hinder border of the gland, and open in *Chiton discrepans* into the pallial groove between the thirteenth and fourteenth gill, in a line with the opening of the renal duct. The duct passes dorsal to the anterior end of the dilated part of the renal duct (fig. 1, *g.d.*), and then curls round the outer border of the lateral nerve cord to its opening, presenting in this respect precisely the same relation as does the renal duct. The male duct has a short direct course to its opening (fig. 1), while the female duct is much coiled.

Another species, *Chiton cancellatus,* which I have examined, presents essentially the same arrangement of its renal organ and generative ducts as that just described for *Chiton discrepans.*

Dall[1] states that in some species of Chiton the generative products escape into the body cavity and make their exit by several pores placed close together, and symmetrically, on each side in the pallial groove; oviducts apparently being

---

[1] 'Proceedings of the United States' National Museum,' vol. i.

absent. I have not any specimens of the species he mentions as possessing this peculiarity (*e.g. Chiton marmoreus* and *ruber*), so have not been able to test his observations by means of sections.

On the GERMINAL LAYERS *and* EARLY DEVELOPMENT *of the* MOLE. By WALTER HEAPE.

THE following is a note on some investigations which I have been carrying on by the kindness and with the help of Mr. Balfour, in the Morphological Laboratory, Cambridge, upon the origin and formation of the germinal layers in mammals, more especially in the mole (*Talpa Europea*). I hope shortly to be able to give a more complete account.

In the communication the following subjects are dealt with:

(1.) The origin of the epiblast.
(2.) The mode of development of the mesoblast.
(3.) The structure of the neurenteric canal.
(4.) The relations of the mesoblast and the hypoblast to the notochord.

Recent investigations have left the earlier phases of mammalian development in some confusion, it may therefore be advisable briefly to mention the more important views which are entertained on this subject.

Professor Edward van Beneden, in a paper entitled "La formation des feuillets chez de Lapin" ('Archives de Biologie,' vol. i, Part 1, 1880), gives an account of the segmentation of the ovum of that animal, and states that during segmentation a differentiation of the segmentation spheres into two layers is established, the one of which grows over and encloses the other, giving rise in this manner to what Van Beneden calls a metagastrula. The outer of these two layers he terms ectoderm and the inner entoderm, names which seem to me, for reasons which will appear in the sequel, to be misleading, and for which I propose to substitute the terms outer and inner layers respectively.

Subsequently, according to Van Beneden, a cavity, the blastodermic cavity, is developed between the outer and inner layers of cells; the cells of the former layer become flattened and multiply, and form the wall of the so-called blastodermic vesicle; at the same time the blastodermic cavity is enlarged, while the inner layer remains as a rounded mass of cells attached to the wall of the vesicle over a small area known as the embryonic area. Van Beneden considers that the outer layer of cells forms the permanent epiblast, both of the embryonic area and of the blastodermic vesicle, while the inner mass of cells breaks up into two layers, a lower single layer of flattened cells, the hypoblast, and a layer of cells which he calls the mesoblast, lying between the hypoblast and the epiblast of the embryonic area.

Professor Kölliker, on the other hand, writing in the 'Zoologischer Anzeiger' (Nos. 61 and 62, vol. iii, 1880), "Die Entwicklung der Keimblätter des Kaninchens," does not dispute the presence of Van Beneden's epiblast, hypoblast, and mesoblast, in the stage of development described above, but states his agreement with an earlier view of Raüber, that in the region of the embryo the outer of these layers disappears, while the whole of the middle layer becomes converted into the epiblast of the embryonic area; the epiblast of the remainder of the vesicle, however, he considers is formed from part of the original outer layer of cells. The mesoblast owes its origin, in his opinion, wholly to a budding from the epiblast of the primitive streak.

Professor Lieberkühn published in Marburg, in 1879, in a paper "Ueber die Keimblätter der Säugethiere," the results of his researches upon the dog and mole, in which he states that the epiblast of the embryonic area is derived from the greater part of the primitive inner mass of cells (that portion in fact forming Van Beneden's mesoblast), together with the part of the original outer layer of cells which overlies the inner mass; the hypoblast he derives from the inner mass of cells, while the mesoblast he believes to be formed from both epiblast and hypoblast in the region of the primitive streak.

I myself have been fortunate enough to secure a fairly complete series of mole embryos ranging from an early appearance of the blastodermic cavity until the formation of the medullary groove; an examination of which leads me, in the main, to agree with Lieberkühn's account of the development of the embryonic layers of that animal.

I have not been able to follow completely the course of segmentation, nor have I been able to trace a differentiation of the segments into two layers, an outer and an inner, though there appears to be no doubt, on account of the arrangement of the spheres in a somewhat later stage, that Van Beneden's description of a fully segmented ovum is substantially correct.

The earliest specimen of an ovum in my possession after the completion of segmentation is similar to that figured in Van Beneden's paper (loc. cit.), Plate iv, fig. 6, iii, and in Lieberkühn's paper (loc. cit.), fig. 1.

The ovum consists of an outer layer and an inner mass of cells, between and partly separating which is a cavity. The outer layer has the form of a sphere of somewhat flattened cells, while the inner mass is composed of irregularly polygonal cells; these two are attached together for a small area, elsewhere they are separated by a cavity, the blastodermic cavity, which is seen in optical section as a crescent-shaped space partially surrounding the inner mass of cells. The diameter of this ovum measures ·11 mm., and that of the inner mass of cells ·06 mm. A thick zona invests the ovum.

Upon the formation of the blastodermic cavity the ovum may be called the blastodermic vesicle.

The vesicle becomes enlarged, and I am inclined to believe that during the enlargement the cells of the inner mass assist in the formation of the outer wall of the vesicle, since in various vesicles of about ·2, ·25, ·3, ·38, mm. diameter, the diameter of the inner mass, which is of an approximately spherical shape, is less, being respectively ·04, ·04, ·04, ·05 mm., than in the youngest vesicle, measuring as stated above, ·11 mm. in which the inner mass is ·06 mm. diameter.

Sections through a vesicle measuring ·25 mm. diameter (the inner mass measuring about ·04 mm.) show the outer layer to be composed of greatly flattened cells closely applied to the zona, which is now much thinner, owing to the expansion of the vesicle, while the inner mass in the form of a solid mass of irregularly rounded cells is attached to the outer layer for a small circular region, which I shall speak of as the embryonic area.

As the vesicle enlarges the inner mass of cells slightly flattens out and widens at the same time, so that the embryonic area becomes enlarged.

In a vesicle ·44 mm. diameter the inner mass of cells is seen to be commencing to divide into two layers, and in a vesicle ·57 mm. in diameter, in which the inner mass is ·08 mm. in diameter, this division is completed, and a layer composed of a single row of slightly flattened cells is separated off from and underlies the main portion of the inner mass of cells; this layer is the hypoblast. The main portion of the inner mass of cells is undergoing at the same time a change in structure, inasmuch as some of the polygonal or rounded cells of which it has hitherto been composed now become elongated and columnar.

The hypoblast in an oval blastodermic vesicle of about ·88 mm. by ·81 mm., is still formed of slightly flattened cells beneath the embryonic area, but it has grown and extended beyond that area, so that its outer part lies beneath and in close contact with the outer layer of the blastodermic vesicle; the cells of this portion of the hypoblast are wide and much flattened, and their nuclei stain deeply with hæmatoxylin.

A cavity appears about this stage of development in the region of the embryonic area between the flattened outer layer and the inner mass, the cells of the latter having now largely become columnar. In the vesicle last mentioned (·88 mm. by ·81 mm.), nearly the whole of the inner mass has become transformed from a rounded mass of polygonal cells into a concave plate of columnar cells, forming the floor of a cavity which is roofed over by the cells of the outer layer of the blastodermic vesicle. In this cavity a few cells are placed, which are connected with the outer layer or inner mass, or with both of these, by means of protoplasmic processes; I believe these cells to be cells of the inner mass which have not yet become columnar.

Lieberkühn states that some of the cells of the inner mass grow round and above the cavity just described, which thus comes to lie within the inner mass. The specimens from which he derives his opinion, however, were, I believe, preserved in Müller's fluid. I have myself seen a similar apparent arrangement in such preparations, which upon comparison with sections of vesicles of similar ages prepared in picric acid appear to me to bear a different interpretation, the layer of cells above the cavity being formed of the flat outer layer cells with a few more or less isolated cells of the inner mass.

In a vesicle of about ·97 mm. diameter the inner mass of cells has still the form of a concave plate composed of two or three layers of for the most part columnar cells; the flattened cells of the outer layer remain, as in the previously described specimen, closely attached to the zona, and the cells lying in the cavity are fewer, while some of them appear to have been drawn on to the concave plate and transformed into columnar cells. Cells in a transition stage may be seen on the surface of the plate.

At a later stage the concave plate extends itself, the curvature becoming less, and eventually approaches to and finally comes into contact with the flat cells forming that portion of the wall of the vesicle which in the previously described specimens lay above the plate; the flattened cells of this part soon become columnar and the fusion between them and the plate becomes complete.

Somewhat prior to this stage the edges of the plate become continuous with the outer layer of the wall of the vesicle beyond the region of the embryonic area.

Thus, the greater part of the inner mass of cells, as Lieberkühn correctly states, combines in the form of a plate of more or less columnar cells with that part of the flat outer layer of cells which immediately overlies it, to form a plate of columnar cells two and three rows deep; this plate is the epiblast plate of the embryonic area, the remainder of the outer layer of cells forming the epiblastic wall of the blastodermic vesicle.

The portion of the inner mass of cells which was separated off from the main mass as the hypoblast still forms only a single row of somewhat rounded cells, the central part of which underlies the embryonic area, while the peripheral part continually extends as a layer of flattened cells along the inner aspect of the epiblastic wall of the remainder of the blastodermic vesicle.

In concluding this portion of my subject I may add, in support of what I believe in harmony with Lieberkühn to be the origin of the true epiblast of the embryonic area in the mole, that in the course of my work on this subject, carried on since the investigations of Mr. Balfour and myself, published in the second volume of Mr. Balfour's 'Comparative Embryology,' I have obtained from an embryo rabbit of six days four hours old, sections which appear to me conclusively to confirm the results at which we before arrived, namely, that the epiblast plate of the embryonic area is derived (as in the mole) conjointly from the at first flattened cells of the primitive outer layer (called by Rauber and Kölliker "Deckzellen," and stated by those observers to disappear from the embryonic area), and from the larger portion of the primitive inner mass of cells (held by Van Beneden to be the true mesoblast, and stated by Kölliker alone to form the epiblast plate. In the sections of this embryo the cells of the already described primitive outer layer are seen in a transition stage, being wedge-shaped and prolonged in between the cells of the inner mass.

At the stage of growth now arrived at the blastodermic vesicle may be considered to consist of an embryonic and a non-embryonic portion. A surface view shows the embryonic area to be in the form of a more or less circular opaque disk. The wall of the vesicle consists of a two-layered and a single-layered portion; the latter, formed of epiblast, alone comprises the portion of the wall opposite to the embryonic area, while the former, consisting of epiblast and hypoblast, forms the embryonic area and the part of the vesicle immediately adjoining it.

In the course of further growth the vesicle greatly enlarges, and the zona becomes much attenuated, affording but little support to the now also exceedingly thin and delicate wall of the vesicle; it therefore becomes difficult to obtain specimens in good preservation.

In the earliest specimen of this stage which I possess the embryonic area is oval, measuring ·74 by ·48 mm. In a surface view a dark line or band is seen to run along the centre of the hinder third of the area. This is the well-known primitive streak; it is narrow anteriorly, while posteriorly it becomes broader, and finally behind takes up nearly the whole breadth of the embryonic area; it is due to the presence of a third layer of cells, the mesoblast, between the epiblast and hypoblast. Transverse sections of this embryonic area show the major portion in front of the primitive streak to be composed (1) of a plate of epiblast formed of two or three rows of columnar cells, and (2) of a single layer of rounded hypoblast cells somewhat flattened towards the edge of the area. Immediately in front of the primitive streak there appears, extending entirely across the area, a layer of mesoblast, which is not connected with the epiblast, but is so intimately united with the hypoblast in the middle line, that the two layers cannot there be clearly distinguished, though towards the periphery of the area they are quite distinct. A section taken through the anterior end of the primitive streak discovers a narrow band of epiblast cells in the middle line, giving rise by budding to a layer of mesoblast which extends laterally to the edge of the area, and in each section following (*i.e.* towards the hind end of the primitive streak) the budding epiblast appears continually as a wider band until the greater part of the whole breadth of the epiblast plate is concerned in the production of mesoblast. A pit is seen in the epiblast almost at the front end of the primitive streak, and at this point a neurenteric canal will eventually be formed; this structure, hitherto overlooked in mammalian embryos, is identical with the neurenteric canal found in other types of Vertebrata.

The primitive streak grows relatively longer compared with the increase in size of the embryonic area, until in a vesicle, in which the latter measures about ·84 by ·71 mm., the primitive streak reaches along it fully three parts of its length. It is very narrow in front, while behind it occupies the whole breadth of the embryonic area. In sections of the region in front of the primitive streak there is present a layer of cells several rows thick immediately underlying the epiblast plate. In the seven anterior sections this layer is seen beneath the epiblast as a mass which cannot be resolved into hypoblast and mesoblast: for about three following sections, placed immediately in front of the primitive streak, the layer is clearly composed of (1) a layer of flattened hypoblast below and (2) a layer of mesoblast above. The mesoblast in the axial line is thickened in the last two of these sections, and posteriorly joins the anterior wall of the neurenteric canal, while the hypoblast extends as a distinct layer below the anterior end of the primitive streak. It appears highly probable that the whole layer in the seven sections at the front end of the embryonic area is the hypoblast originally present there engaged in the act of budding off mesoblast, as Balfour believes to be the case with regard to a similarly situated portion of the hypoblast in the chick ('Comparative Embryology,' vol. ii, p. 129 *et. seq.*). In the three following sections where distinct layers of mesoblast and hypoblast are found, the whole of the mesoblast, with the exception of the cells forming the central thickening in the second and third sections, has, I believe, a similar origin, and may be distinguished by the form and appearance of its cells from the mesoblast of the primitive streak. The mesoblast derived from the hypoblast may be called hypoblastic mesoblast; it joins the mesoblast of the primitive streak as the latter grows forward, and the two become indistinguishable.

The primitive streak presents in section a similar appearance to that of the embryo last described; a groove—the primitive groove—is, however, present along its upper surface. The position of the future neurenteric canal is indicated by a pit in the epiblast as in the specimen described above.

At a slightly later stage the embryonic area being 1·17 by ·81 mm., the condition of the layers is much the same. A neurenteric canal now perforates the whole thickness of the blastoderm at the front end of the primitive groove. The upper opening of this canal, which is longer than the lower opening, has the appearance of a slit with its anterior wall sloping obliquely backwards; this wall is continuous with the thickening of mesoblast cells in the axial line which I described in the last stage. The first traces of the amnion are now visible as a fold of the epiblast round the whole circumference of the embryonic area; at the posterior end the folds of the two sides meet to form a hood, covering the hinder part of the area, but anteriorly I have been unable to determine the extent of their growth.

In the surface view of an embryonic area measuring ·97 by 79 mm. in diameter, a band of a lighter shade than the remainder is to be seen in the front part of the long axis of the area, its posterior end adjoining the anterior end of the primitive streak; the latter occupies the hinder third of the area, and where it joins the light-coloured band a pit, the upper opening of the neurenteric canal, is distinctly to be seen surrounded by a dark rim.

In transverse section the light-coloured band is seen to be caused by a diminution in thickness of the epiblast plate and of the mesoblast in the middle line. The epiblast of this region is bent inwards to form a groove, the medullary groove; it is wide and shallow throughout, and the cells forming it are not more than two rows deep, while the remainder of the epiblast plate, except at the extreme edge, is three cells deep.

Anterior to the medullary groove a continuous layer hardly differentiated into mesoblast and hypoblast underlies the epiblast plate. In the region of the medullary groove an axial strip of the cells underlying the epiblast exhibits no division into hypoblast and mesoblast; this portion, though partially separated from the lateral masses of mesoblast, is still connected with them, however, on each side by a narrow neck of cells, and is also directly continuous laterally with the hypoblast. The lateral hypoblast is quite distinct from the superjacent lateral masses of mesoblast. The axial strip of cells underlying the medullary groove (thus shown to be continuous with both the mesoblast and the hypoblast) may be regarded as the commencing notochord.

The neurenteric canal does not any longer perforate the blastoderm, its upper part alone remaining, which is surrounded by a thick mass of mesoblast, causing the dark rim seen in the surface view round the pit. Its anterior wall is connected with the axial mass of cells underlying the medullary groove, while its hind wall forms the front end of the primitive streak.

The surface view of a somewhat older specimen, 1·5 mm. by ·81 mm. diameter, shows the medullary groove relatively much longer and more clearly defined. Anteriorly it reaches nearly to the edge of the embryonic area.

In section it is seen to be shallow at each end, but is much deeper and narrower towards the middle of the embryonic area. Its walls, at the anterior end, are but slightly less thick than the remainder of the epiblast plate, but in the deeper part of the groove become considerably thinner. Where the groove is deepest the notochord and adjacent parts form a well-marked projection into the blastodermic cavity beneath.

The rudimentary notochord has now extended beyond the anterior end of the medullary groove, and its relations to the adjacent layers are, for the most part, the same as in the previously described specimen. In front of the medullary groove it is composed of a single row of somewhat columnar cells, continuous laterally with both mesoblast and hypoblast; below the anterior more shallow part of the medullary groove similar relations exist, towards its middle and deeper part, however, where the lateral mesoblast is commencing to form protovertebræ, the notochordal cells, still in the form of a single row, are connected solely with the lateral plates of hypoblast, while further back, where the medullary groove becomes again more shallow, the cells of the notochord become more than one row deep, and are again continuous both with the lateral mesoblast and hypoblast. The notochord, continually thickening towards its hinder extremity, terminates by fusing with the anterior wall of the neurenteric canal. The latter structure is now open above on the floor of the posterior end of the medullary groove, and extends downwards into the cells beneath, though it no longer perforates the hypoblast, which is, however, somewhat involuted, and indistinguishably fused with the mesoblast in the median line.

Briefly to recapitulate, I have attempted to show:

(1.) The epiblast of the blastodermic vesicle owes its origin as well to the inner mass of segmentation spheres as to the outer layer of segments. It appears to originate in two ways:

(*a.*) In an early stage of development (in the mole) probably by the cells of the inner mass being directly transformed into part of the wall of the blastodermic vesicle.

(*b.*) In a later stage (mole and rabbit) by the transformation of the rounded cells of the inner mass into a plate of columnar cells, which joins the part of the outer layer lying immediately above it to form the epiblast plate of the embryonic area.

(2.) The mesoblast in the mole is formed in two portions:

(*a.*) A larger portion which has its origin in the primitive streak.

(*b.*) A smaller portion which is derived from the hypoblast situated in front of the primitive streak.

I have been unable to distinguish where the latter, or hypoblastic mesoblast, comes into contact with the mesoblast of the primitive streak, and what part these respective layers take in the future development of the embryo.

(3.) A neurenteric canal is present in the mole similar to that formed in other types of Vertebrata, first appearing as a pit at the anterior end of the primitive streak, while in later stages it perforates the floor of the hinder end of the medullary groove.

I may here add that I have also found in a seven days' rabbit embryo a rudimentary neurenteric canal in the form of a shallow pit in the epiblast at the front end of the primitive streak.

(4.) The notochord is formed of an axial strip of cells, which underlies the epiblast of the medullary groove, and which either never becomes divided into mesoblast and hypoblast, or in which such a division, if it does take place (as appears not impossible), is very soon lost. This strip of cells is originally continuous laterally with both mesoblast and hypoblast, but as the lateral mesoblast becomes converted into definite vertebral plates the connection is lost.

There can, I believe, be no doubt of the connection of the lateral hypoblast and mesoblast with the notochordal cells in the mole; in the rabbit I am inclined to believe that a similar connection is present, but my evidence on this point is not yet conclusive.

PRINTED BY J. E. ADLARD, BARTHOLOMEW CLOSE.

A RENEWED STUDY *of the* GERMINAL LAYERS *of the* CHICK. By F. M. BALFOUR, LL.D., F.R.S., Trinity College, Cambridge, and F. DEIGHTON, B.A., St. Peter's College. (With Plates VII, VIII and IX.)

THE formation of the germinal layers in the chick has been so often and so fully dealt with in recent years, that we consider some explanation to be required of the reasons which have induced us to add to the long list of memoirs on this subject. Our reasons are twofold. In the first place the principal results we have to record have already been briefly put forward in a 'Treatise on Comparative Embryology' by one of us; and it seemed desirable that the data on which the conclusions there stated rest should be recorded with greater detail than was possible in such a treatise. In the second place, our observations differ from those of most other investigators, in that they were primarily made with the object of testing a theory as to the nature of the primitive streak. As such they form a contribution to comparative embryology; since our object has been to investigate how far the phenomena of the formation of the germinal layers in the chick admit of being compared with those of lower and less modified vertebrate types.

We do not propose to weary the reader by giving a new version of the often told history of the views of various writers on the germinal layers in the chick, but our references to other investigators will be in the main confined to a comparison of our results with those of two embryologists, who have published their memoirs since our observations were made. One of them is L. Gerlach, who published a short memoir[1] in April last, and the other is C. Koller, who has published his memoir[2] still more recently. Both of them cover part of the ground of our investi-

---

[1] "Ueb. d. entodermale Entstehungswiese d. Chorda dorsalis," 'Biol. Centralblatt,' vol. i, Nos. 1 and 2.

[2] "Untersuch. üb. d. Blätterbildung im Hühnerkeim," 'Archiv. f. mikr. Anat.,' vol. xx, 1881.

gations, and their results are in many, though not in all points, in harmony with our own. Both of them, moreover, lay stress on certain features in the development which have escaped our attention. We desired to work over these points again, but various circumstances have prevented our doing so, and we have accordingly thought it best to publish our observations as they stand, in spite of their incompleteness, merely indicating where the most important gaps occur.

Our observations commence at a stage a few hours after hatching, but before the appearance of the primitive streak.

The area pellucida is at this stage nearly spherical. In it there is a large oval opaque patch, which is continued to the hinder border of the area. This opaque patch has received the name of the embryonic shield—a somewhat inappropriate name, since the structure in question has no very definite connection with the formation of the embryo.

Koller describes, at this stage, in addition to the so-called embryonic shield, a sickle-shaped opaque appearance at the hinder border of the area pellucida.

We have not made any fresh investigations for the purpose of testing Koller's statements on this subject.

Embryologists are in the main agreed as to the structure of the blastoderm at this stage. There is (Pl. VII, Ser. A, 1 and 2) the epiblast above, forming a continuous layer, extending over the whole of the area opaca and area pellucida. In the former its cells are arranged as a single row, and are cubical or slightly flattened. In the latter the cells are more columnar, and form, in the centre especially, more or less clearly, a double row; many of them, however, extend through the whole thickness of the layer.

We have obtained evidence at this stage which tends to show that at its outer border the epiblast grows not merely by the division of its own cells, but also by the addition of cells derived from the yolk below. The epiblast has been observed to extend itself over the yolk by a similar process in many invertebrate forms.

Below the epiblast there is placed, in the peripheral part of the area opaca, simply white yolk; while in a ring immediately outside and concentric with the area pellucida, there is a closely-packed layer of cells, known as the *germinal wall*. The constituent cells of this wall are in part relatively small, of a spherical shape, with a distinct nucleus, and a granular and not very abundant protoplasm; and in part large and spherical, filled up with highly refracting yolk particles of variable size, which usually render the nucleus (which is probably present) invisible (A, 1 and 2). This mass of cells rests, on its outer side, on a layer of white yolk.

The sickle-shaped structure, visible in surface veins, is stated by Koller to be due to a special thickening of the germinal wall. We have not found this to be a very distinctly marked structure in our sections.

In the region of the area pellucida there is placed below the epiblast a more or less irregular layer of cells. This layer is continuous, peripherally, with the germinal wall; and is composed of cells, which are distinguished both by their flattened or oval shape and more granular protoplasm from the epiblast-cells above, to which, moreover, they are by no means closely attached. Amongst these cells a few larger cells are usually present, similar to those we have already described as forming an important constituent of the germinal wall.

We have figured two sections of a blastoderm of this age (Ser. A, 1 and 2) mainly to show the arrangement of these cells. A large portion of them, considerably more flattened than the remainder, form a continuous membrane over the whole of the area pellucida, except usually for a small area in front, where the membrane is more or less interrupted. This layer is the hypoblast (*hy.*). The remaining cells are interposed between this layer and the epiblast. In front of the embryonic shield there are either comparatively few or none of these cells present (Ser. A, 1), but in the region of the embryonic shield they are very numerous (Ser. A, 2), and are, without doubt, the main cause of the opacity of this part of the area pellucida. These cells may be regarded as not yet completely differentiated segmentation spheres.

In many blastoderms, not easily distinguishable in surface views from those which have the characters just described, the hypoblastic sheet is often much less completely differentiated, and we have met with other blastoderms, again, in which the hypoblastic sheet was completely established, except at the hinder part of the embryonic shield; where, in place of it and of the cells between it and the epiblast, there was only to be found a thickish layer of rounded cells, continuous behind with the germinal wall.

In the next stage, of which we have examined surface views and sections, there is already a well-formed primitive streak.

The area pellucida is still nearly spherical, the embryonic shield has either disappeared or become much less obvious, but there is present a dark linear streak, extending from the posterior border of the area pellucida towards the centre, its total length being about one third, or even less, of the diameter of the area. This streak is the *primitive streak.* It enlarges considerably behind, where it joins the germinal wall. By Koller and Gerlach it is described as joining the sickle-shaped structure already spoken of. We have in some instances found the posterior end of the primitive streak extending laterally in the form of two wings (Pl. IX, fig. L). These extensions are, no doubt, the sickle; but the figures given by Koller appear to us somewhat diagrammatic. One or two of the figures of early primitive streaks in the sparrow, given by Kupffer and Benecke,[1] correspond more closely with what we have found, except that in these figures the primitive streak does not reach the end of the area pellucida, which it certainly usually does at this early stage in the chick.

Sections through the area pellucida (Pl. VII, ser. B and C) give the following results as to the structure of its constituent parts.

The epiblast cells have undergone division to a considerable extent, and in the middle part, especially, are decidedly more columnar than at an earlier stage, and distinctly divided into two rows, the nuclei of which form two more or less distinct layers.

In the region in front of the primitive streak the cells of the lower part of the blastoderm have arranged themselves as a definite layer, the cells of which are not so flat as is the case with the hypoblast cells of the posterior part of the blastoderm, and in the older specimens of this stage they are very decidedly more columnar than in the younger specimens.

The primitive streak is however the most interesting structure in the area pellucida at this stage.

The feature which most obviously strikes the observer in transverse sections through it is the fact, proved by Kölliker, that it is mainly due to a proliferation of the epiblast cells along an axial streak, which, roughly speaking, corresponds with the dark line visible in surface views. In the youngest specimens and at the front end of the primitive streak, the proliferated cells do not extend laterally beyond the region of their origin, but in the older specimens they have a considerable lateral extension.

The hypoblast can, in most instances, be traced as a distinct layer underneath the primitive streak, although it is usually less easy to follow it in that region than elsewhere, and in some cases it can hardly be distinctly separated from the superjacent cells.

The cells undoubtedly formed by a proliferation of the epiblast, form a compact mass extending downwards towards the hypoblast; but between this mass and the hypoblast there are almost always present along the whole length of the primitive streak a number of cells, more or less loosely arranged, and

---

[1] "Photogramme d. Ontogenie d. Vogel." Nova Acta. K. Leop. Carol, 'Deutschen Akad. d. Naturfor.,' Bd. x, 41, 1879.

decidedly more granular than the proliferated cells. Amongst these loosely arranged cells there are to be found a certain number of large spherical cells filled with yolk granules. Sometimes these cells are entirely confined to the region of primitive streak, at other times they are continuous laterally with cells irregularly scattered between the hypoblast and epiblast (Ser. C, 2), which are clearly the remnants of the undifferentiated cells of the embryonic shield. The junction between these cells and the cells of the primitive streak derived from the epiblast is often obscure, the two sets of cells becoming partially intermingled. The facility with which the cells we have just spoken of can be recognised varies moreover greatly in different instances. In some cases they are very obvious (Ser. C), while in other cases they can only be distinguished by a careful examination of good sections.

The cells of the primitive streak between the epiblast and the hypoblast are without doubt mesoblastic, and constitute the first portion of the mesoblast which is established. The section of these cells attached to the epiblast, in our opinion, clearly originates from the epiblast; while the looser cells adjoining the hypoblast must, it appears to us, be admitted to have their origin in the indifferent cells of the embryonic shield, placed between the epiblast and the hypoblast, and also very probably in a distinct proliferation from the hypoblast below the primitive streak.

Posteriorly the breadth of the streak of epiblast which buds off the cells of the primitive streak widens considerably, and in the case of the blastoderm with the earliest primitive streaks extends into the region of the area opaca. The widening of the primitive streak behind is shown in Ser. B, 3; Ser. C, 2; and Ser. E, 4. Where very marked it gives rise to the sickle-shaped appearance upon which so much stress has been laid by Koller and Gerlach. In the case of one of the youngest of our blastoderms of this stage in which we found in surface views (Pl. IX, fig. L) a very well-marked sickle-shaped appearance at the hind end of the primitive streak, the appearance was caused, as is clearly brought out by our sections, by a thickening of the hypoblast of the germinal wall.

There is a short gap in our observations between the stage with a young primitive streak and the first described stage in which no such structure is present. This gap has been filled up both by Gerlach and Koller.

Gerlach states that during this period a small portion of the epiblast, within the region of the area opaca, but close to the posterior border of the area pellucida, becomes thickened by a proliferation of its cells. This portion gradually grows outwards laterally, forming in this way a sickle-shaped structure. From the middle of this sickle a process next grows forward into the area pellucida. This process is the primitive streak, and it is formed, like the sickle, of proliferating epiblast cells.

Koller[1] described the sickle and the growth forwards from it of the primitive streak in surface views somewhat before Gerlach; and in his later memoir has entered with considerable detail into the part played by the various layers in the formation of this structure.

He believes, as already mentioned, that the sickle-shaped structure, which appears according to him at an earlier stage than is admitted by Gerlach, is in the first instance due to a thickening of the hypoblast. At a later stage he finds that the epiblast in the centre of the sickle becomes thickened, and that a groove makes its appearance in this thickening which he calls the "Sichel-rinne." This groove is identical with that first described by Kupffer and Benecke[2] in the sparrow and fowl. We have never, however, found very clear indications of it in our sections.

In the next stage, Koller states that, in the region immediately in front of the "Sichel-rinne," a prominence appears which he calls the Sichelknopf, and from this a process grows forwards which constitutes the primitive streak. This structure is in main derived from a proliferation of epiblast cells, but Koller admits that some of the cells just above the hypoblast in the region of the Sichelknopf are probably derived from the hypoblast. Since these cells form part of the mesoblast it is obvious that Koller's views on the origin of the mesoblast of the primitive streak closely approach those which we have put forward.

The primitive streak starting, as we have seen, at the hinder border of the area pellucida, soon elongates till it eventually occupies at least two thirds of the length of the area. As Koller (loc. cit.) has stated this can only be supposed to happen in one of two ways, viz. either by a progression forward of the region of epiblast budding off mesoblast, or by an interstitial growth of area of budding epiblast. Koller adopts the second of these alternatives, but we cannot follow him in doing so. The simplest method of testing the point is by measuring the distance between the front end of the primitive streak and the front border of the area pellucida at different stages of growth of the primitive streak. If this distance diminishes with the elongation of the primitive streak then clearly the second of the two alternatives is out of the question.

We have made measurements to test this point, and find that the diminution of the space between the front end of the

---

[1] "Beitr. z. Kenntniss d. Hühnerkeims im Beginne d. Bebrütung," 'Sitz. d. k. Akad. Wiss.,' iv Abth., 1879.

[2] 'Die erste Entwick. an Eier d. Reptilien.' Königsberg, 1878.

primitive streak and the anterior border of the area pellucida is very marked up to the period in which the medullary plate first becomes established. We can further point in support of our view to the fact that the extent of the growth lateralwards of the mesoblast from the sides of the primitive streak is always less in front than behind; which would seem to indicate that the front part of the streak is the part formed latest. Our view as to the elongation of the primitive streak appears to be that adopted by Gerlach.

Our next stage includes roughly the period commencing slightly before the first formation of a groove along the primitive streak, known as the primitive groove, and terminating immediately before the first trace of the notochord makes its appearance. After the close of the last stage the primitive streak gradually elongates, till it occupies fully two thirds of the diameter of the area pellucida. The latter structure also soon changes its form from a circular to an oval, and finally becomes pyriform with the narrow end behind, while the primitive streak occupying two thirds of its long axis becomes in most instances marked by a light linear band along the centre, which constitutes the primitive groove.

In surface views the primitive streak often appears to stop short of the hinder border of the area pellucida.

During the period in which the external changes, which we have thus briefly described, take place in the area pellucida, great modifications are effected in the characters of the germinal layers. The most important of these concern the region in front of the primitive streak; but they will be better understood if we commence our description with the changes in the primitive streak itself.

In the older embryos belonging to our last stage we pointed out that the mesoblast of the primitive streak was commencing to extend outwards from the median line in the form of two lateral sheets. This growth of the mesoblast is continued rapidly during the present stage, so that during the latter part of it any section through the primitive streak has approximately the characters of Ser. I, 5.

The mesoblast is attached in the median line to the epiblast. Laterally it extends outwards to the edge of the area pellucida, and in older embryos may even form a thickening beyond the edge (fig. G). Beneath the denser part of the mesoblast, and attached to the epiblast, a portion composed of stellate cells may in the majority of instances be recognised, especially in the front part of the primitive streak. We believe these stellate cells to be in the main directly derived from the more granular cells of the previous stage. The hypoblast forms a sheet of flattened cells, which can be distinctly traced for the whole breadth of the area pellucida, though closely attached to the mesoblast above.

In sections we find that the primitive streak extends back to the border of the area pellucida, and even for some distance beyond. The attachment to the epiblast is wider behind; but the thickness of the mesoblast is not usually greater in the median line than it is laterally, and for this reason probably the posterior part of the streak fails to show up in surface views. The thinning out of the median portion of the mesoblast of the primitive streak is shown in a longitudinal section of a duck's blastoderm of this stage (fig. D). The same figure also shows that the hypoblastic sheet becomes somewhat thicker behind, and more independent of the parts above.

A careful study of the peripheral part of the area pellucida, in the region of the primitive streak, in older embryos of this stage, shows that the hypoblast is here thickened, and that its upper part, *i.e.* that adjoining the mesoblast, is often formed of stellate cells, many of which give the impression of being in the act of passing into the mesoblast above. At a later stage the mesoblast of the vascular area undoubtedly receives accessions of cells from the yolk below; so that we see no grounds for mistrusting the appearances just spoken of, or for doubting that they are to be interpreted in the sense suggested.

We have already stated that during the greater part of the present stage a groove, known as the primitive groove, is to be found along the dorsal median line of the primitive streak.

The extent to which this groove is developed appears to be subject to very great variation. On the average it is, perhaps, slightly deeper than it is represented in Ser. I, 5. In some cases it is very much deeper. One of the latter is represented in fig. G. It has here the appearance of a narrow slit, and sections of it give the impression of the mesoblast originating from the lips of a fold; in fact, the whole structure appears like a linear blastopore, from the sides of which the mesoblast is growing out; and this as we conceive actually to be the true interpretation of the structure. Other cases occur in which the primitive groove is wholly deficient, or at the utmost represented by a shallow depression along the median axial line of a short posterior part of the primitive streak.

We may now pass to the consideration of the part of the area pellucida in front of the primitive streak.

We called attention to a change in the character of the hypoblast cells of this region as taking place at the end of the last stage. During the very early part of this stage the change in the character of these cells becomes very pronounced.

What we consider to be our earliest stage in this change we have only so far met with in the duck, and we have figured a longitudinal and median section to show it (Pl. VII, fig. D). The hypoblast (*hy*) has become a thick layer of somewhat cubical cells several rows deep. These cells, especially in front, are characterised by their numerous yolk spherules, and give the impression that part of the area pellucida has been, so to speak, reclaimed from the tarea opaca. *Posteriorly, at the front end of the primitive streak, the thick layer of hypoblast, instead of being continuous with the flattened hypoblast under the primitive streak, falls, in the axial line, into the mesoblast of the primitive streak* (Pl. VII, fig. D).

In a slightly later stage, of which we have specimens both of the duck and chick, but have only figured selected sections of a chick series, still further changes have been effected in the constitution of the hypoblast (Pl. VIII, Ser. H, 1 and 2).

Near the front border of the area pellucida (1) it has the general characters of the hypoblast of the duck's blastoderm just described. Slightly further back the cells of the hypoblast have become differentiated into stellate cells several rows deep, *which can hardly be resolved in the axial line into hypoblast and mesoblast,* though one can fancy that in places, especially laterally, they are partially differentiated into two layers. The axial sheet of stellate cells is continuous laterally with cubical hypoblast cells.

As the primitive streak is approached an axial prolongation forwards of the rounded and closely-packed mesoblastic elements of the primitive streak is next met with, and at the front end of the primitive streak, where this prolongation unites with the epiblast, it also becomes continuous with the stellate cells just spoken of. In fact, close to the end of the primitive streak it becomes difficult to say which mesoblast cells are directly derived from the primitive layer of hypoblast in front of the primitive streak, and which from the forward growth of the mesoblast of the primitive streak. There is, in fact, as in the earlier stage, a fusion of the layers at this point.

Sections of a slightly older chick blastoderm are represented in Pl. VIII, Ser. I, 1, 2, 3, 4 and 5.

Nearly the whole of the hypoblast in front of the primitive streak has now undergone a differentiation into stellate cells. In the second section the products of the differentiation of this layer form a distinct mesoblast and hypoblast laterally, while in the median line they can hardly be divided into two distinct layers.

In a section slightly further back the same is true, except that we have here, in the axial line above the stellate cells, rounded elements derived from a forward prolongation of the cells of the primitive streak. In the next section figured, passing through the front end of the primitive streak, the axial cells have become continuous with the axial mesoblast of the primitive streak, while below there is an independent sheet of flattened hypoblast cells.

The general result of our observations on the part of the blastoderm in front of the primitive streak during this stage is to show that the primitive hypoblast of this region undergoes considerable changes, including a multiplication of its cells; and that these changes result in its becoming differentiated on each side of the middle line, with more or less distinctness, into (1) a hypoblastic sheet below, formed of a single row of flattened cells, and (2) a mesoblast plate above formed of stellate cells, while in the middle line there is a strip of stellate cells in which there is no distinct differentiation into two layers.

Since the region in which these changes take place is that in which the medullary plate becomes subsequently formed, the lateral parts of the mesoblast plate are clearly the permanent lateral plates of the trunk, from which the mesoblastic somites, &c., become subsequently formed; *so that the main part of the mesoblast of the trunk is not directly derived from the primitive streak.*

Before leaving this stage we would call attention to the presence, in one of our blastoderms of this stage, of a deep pit at the junction of the primitive streak with the region in front of it (Pl. VIII, Ser. F, 1 and 2). Such a pit is unusual, but we think it may be regarded as an exceptionally early commencement of that most variable structure in the chick, the neurenteric canal.

The next and last stage we have to deal with is that during which the first trace of the notochord and of the medullary plate make their appearance.

In surface views this stage is marked by the appearance of a faint dark line, extending forwards, from the front end of the primitive streak, to a fold, which has in the mean time made its appearance near the front end of the area pellucida, and constitutes the head fold.

Pl. IX, Ser. K, represents a series of sections through a blastoderm of this stage, which have been selected to illustrate the mode of formation of the notochord.

In a section immediately behind the head fold the median part of the epiblast is thicker than the lateral parts, forming the first indication of a medullary plate (Ser. K, 1). Below the median line of the epiblast is a small cord of cells, not divided into two layers, but continuous laterally, both with the hypoblast and mesoblast, which are still more distinctly separated than in the previous stage.

A section or so further back (Ser. K, 2) the axial cord, which we need scarcely say is the rudiment of the notochord, is thicker, and causes a slight projection in the epiblast above. It is, as before, continuous laterally, both with the mesoblast and with the hypoblast. The medullary plate is more distinct, and a shallow but unmistakable medullary groove has made its appearance.

As we approach the front end of the primitive streak the notochord becomes (Ser. K, 3) very much more prominent, though retaining the same relation to the germinal layers as in front.

In the section immediately behind (Ser. K, 4) the convex upper surface of the notochord has become continuous with the epiblast for a very small region. The section, in fact, traverses the front end of the primitive streak.

In the next section the attachment between the epiblast and the cells below becomes considerably wider. It will be noticed that this part of the primitive streak is placed on the floor of the wide medullary groove, and there forms a prominence known as the anterior swelling of the primitive streak.

It will further be noticed that in the two sections passing through the primitive streak, the hypoblast, instead of simply becoming continuous with the axial thickening of the cells, as in front, forms a more or less imperfect layer underneath it. This layer becomes in the sections following still more definite, and forms part of the continuous layer of hypoblast present in the region of the primitive streak.

A comparison of this stage with the previous one shows very clearly that the notochord is formed out of the median plate of cells of the earlier stage, which was not divided into mesoblast and hypoblast, together with the short column of cells which grew forwards from the primitive streak.

The notochord, from its mode of origin, is necessarily continuous behind with the axial cells of the primitive streak.

The sections immediately behind the last we have represented show a rudiment of the neurenteric canal of the same form as that first figured by Gasser, viz. a pit perforating the epiblast with a great mass of rounded cells projecting upwards through it.

The observations just recorded practically deal with two much disputed points in the ontogeny of birds, viz. the origin of the mesoblast and the origin of the notochord.

With reference to the first of these our results are briefly as follows:

The first part of the mesoblast to be formed is that which arises in connection with the primitive streak. This part is in the main formed by a proliferation from an axial strip of the epiblast along the line of the primitive streak, but in part also from a simultaneous differentiation of hypoblast cells also along the axial line of the primitive streak. The two parts of the mesoblast so formed become subsequently indistinguishable. The second part of the mesoblast to be formed is that which gives rise to the lateral plates of mesoblast of the head and trunk of the embryo. This part appears as two plates—one on each side of the middle line—which arise by direct differentiation from the hypoblast in front of the primitive streak. They are continuous behind with the lateral wings of mesoblast which grow out from the primitive streak, and on their inner side are also at first continuous with the cells which form the notochord.

In addition to the parts of mesoblast, formed as just described, the mesoblast of the vascular area is in a large measure developed by a direct formation of cells round the nuclei of the germinal wall.

The mesoblast formed in connection with the primitive streak gives rise in part to the mesoblast of the allantois, and ventral part of the tail of the embryo (?), and in part to the vascular structures found in the area pellucida.

With reference to the formation of the mesoblast of the primitive streak, our conclusions are practically in harmony with those of Koller; except that Koller is inclined to minimise the share taken by the hypoblast in the formation of the mesoblast of the primitive streak.

Gerlach, with reference to the formation of this part of the mesoblast, adopts the now generally accepted view of Kölliker, according to which the whole of the mesoblast of the primitive streak is derived from the epiblast.

As to the derivation of the lateral plates of mesoblast of the trunk from the hypoblast of the anterior part of the primitive streak, our general result is in complete harmony with Gerlach's results, although in our accounts of the details of the process we differ in some not unimportant particulars.

As to the origin of the notochord, our main result is that this structure is formed as an actual thickening of the primitive hypoblast of the anterior part of the area pellucida. We find that it unites posteriorly with a forward growth of the axial tissue of the primitive streak, while it is laterally continuous, at first, both with the mesoblast of the lateral plates and with the hypoblast. At a later period its connection with the mesoblast is severed, while the hypoblast becomes differentiated as a continuous layer below it.

As to the hypoblastic origin of the notochord, we are again in complete accord with Gerlach; but we differ from him in admitting that the notochord is continuous posteriorly with the axial tissue of the primitive streak, and also at first continuous with the lateral plates of mesoblast.

The account we have given of the formation of the mesoblast may appear to the reader somewhat fantastic, and on that account not very credible. We believe, however, that if the view which has been elsewhere urged by one of us, that the primitive streak is the homologue of the blastopore of the lower vertebrates is accepted, the features we have described receive an adequate explanation.

The growth outwards of part of the mesoblast from the axial line of the primitive streak is a repetition of the well-known growth from the lips of the blastopore. It might have been anticipated that all the layers would fuse along the line of the primitive streak, and that the hypoblast as well as part of the mesoblast would grow out from it. There is, however, clearly a precocious formation of the hypoblast; but the formation of the mesoblast of the primitive streak, partly from the epiblast and partly from the hypoblast, is satisfactorily explained by regarding the whole structure as the blastopore. The two parts of the mesoblast subsequently become indistinguishable, and their difference in origin is, on the above view, to be regarded as simply due to a difference of position, and not as having a deeper significance.

The differentiation of the lateral plates of mesoblast of the trunk directly from the hypoblast is again a fundamental feature of vertebrate embryology, occurring in all types from Amphioxus upwards, the meaning of which has been fully dealt with in the 'Treatise on Comparative Embryology' by one of us. Lastly, the formation of the notochord from the hypoblast is the typical vertebrate mode of formation of this organ, while the fusion of the layers at the front end of the primitive streak is the universal fusion of the layers at the dorsal lip of the blastopore, which is so well known in the lower vertebrate types.

EXPLANATION OF PLATES VII, VIII & IX,

Illustrating Messrs. Balfour and Deighton's Paper on "A Renewed Study of the Germinal Layers of the Chick."

N.B.—The series of sections are in all cases numbered from before backwards.

List of Reference Letters.

ep. Epiblast. *hy.* Hypoblast. *m.* Mesoblast. *gr.* Germinal wall. *yk.* Yolk of germinal wall. *pv s.* Primitive streak. *pr. g.* Primitive groove. *ch.* Notochord. *a. p.* Area pellucida. *o. p.* Area opaca.

PLATE VII.

Series A, 1 and 2.—Sections through the blastoderm before the appearance of primitive streak.

1. Section through anterior part of area pellucida in front of embryonic shield. The hypoblast here forms an imperfect layer. The figure represents about half the section. 2. Section through same blastoderm, in the region of the embryonic shield. Between the epiblast and hypoblast are a number of undifferentiated cells. The figure represents considerably more than half the section.

Series B, 1, 2 and 3.—Sections through a blastoderm with a very young primitive streak.

1. Section through the anterior part of the area pellucida in front of the primitive streak. 2. Section through about the middle of the primitive streak. 3. Section through the posterior part of the primitive streak.

Series C, 1 and 2.—Sections through a blastoderm with a young primitive streak.

1. Section through the front end of the primitive streak. 2. Section through the primitive streak, somewhat behind 1. Both figures show very clearly the difference in character between the cells of the epiblastic mesoblast of the primitive streak, and the more granular cells of the mesoblast derived from the hypoblast.

Fig. D.—Longitudinal section through the axial line of the primitive streak, and the part of the blastoderm in front of it, of an embryo duck with a well-developed primitive streak.

Series E,[1] 1, 2, 3 and 4.—Sections through blastoderm with a primitive streak, towards the end of the first stage.

1. Section through the anterior part of the area pellucida. 2. Section a little way behind 1 showing a forward growth of mesoblast from the primitive streak. 3. Section through primitive streak. 4. Section through posterior part of primitive streak, showing the great widening of primitive streak behind.

---

[1] 3 and 4 of this series are placed on Plate VIII.

PLATE VIII.

SERIES F, 1 and 2.—Sections through a blastoderm with primitive groove.

1. Section showing a deep pit in front of primitive streak, probably an early indication of the neurenteric canal. 2. Section immediately following 1.

FIG. G.—Section through blastoderm with well developed primitive streak, showing an exceptionally deep slit-like primitive groove.

SERIES H, 1 and 2.—Sections through a blastoderm with a fully-developed primitive streak.

1. Section through the anterior part of area pellucida, showing the cubical granular hypoblast cells in this region. 2. Section slightly behind 1, showing the primitive hypoblast cells differentiated into stellate cells, which can hardly be resolved in the middle line into hypoblast and mesoblast.

SERIES I, 1, 2, 3, 4 and 5.—Sections through blastoderm somewhat older than Series H.

1. Section through area pellucida well in front of primitive streak. 2. Section through area pellucida just in front of primitive streak. 3. Section through the front end of primitive streak. 4. Section slightly behind 3. 5. Section slightly behind 4.

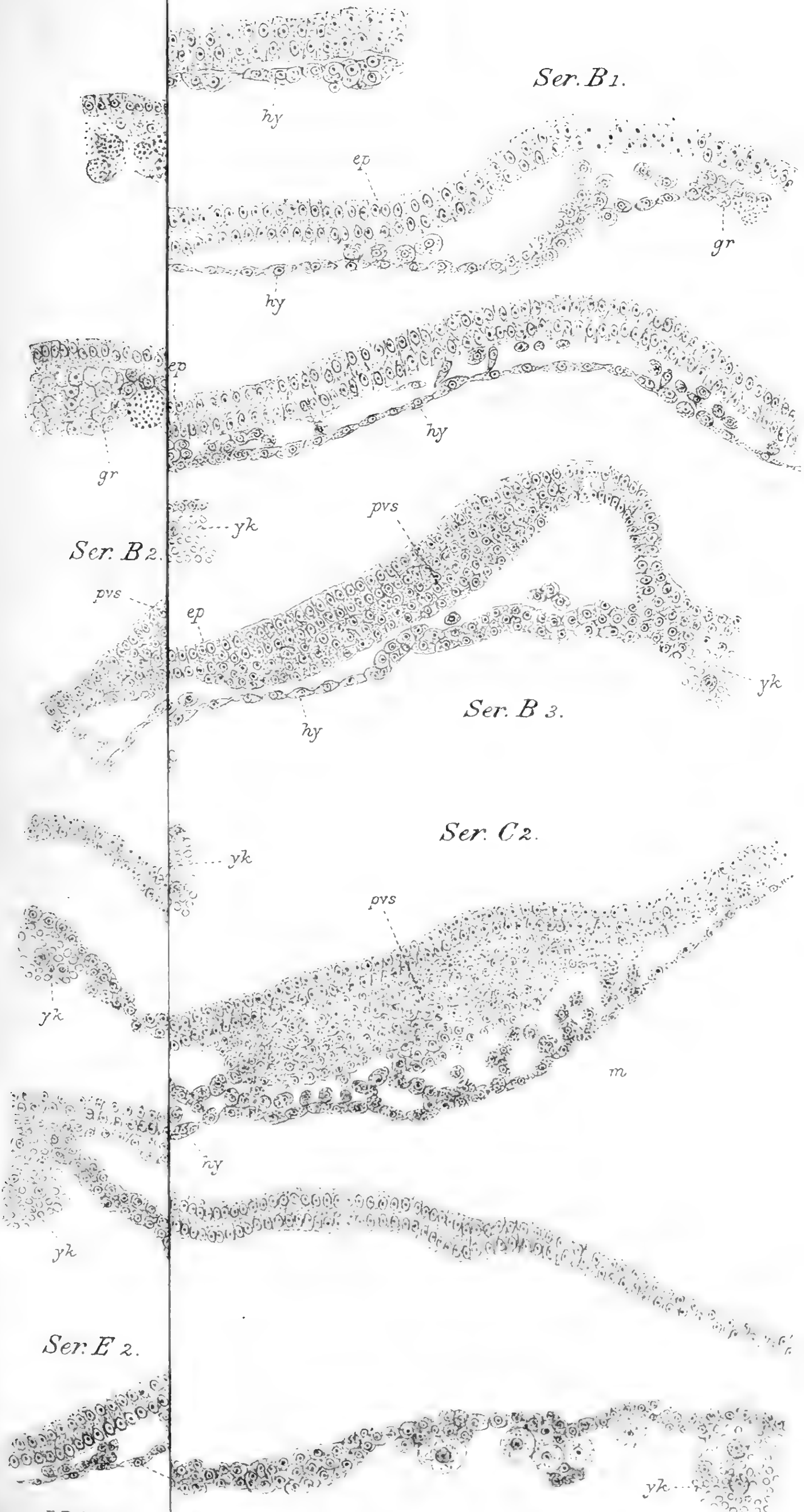
PLATE IX.

SERIES K, 1, 2, 3, 4 and 5.—Sections through a blastoderm in which the first trace of notochord and medullary groove have made their appearance. Rather more than half the section is represented in each figure, but the right half is represented in 1 and 3, and the left in 2 and 4.

1. Section through notochord immediately behind the head-fold. 2. Section showing medullary groove a little behind 1. 3. Section just in front of the primitive streak. 4 and 5. Sections through the front end of the primitive streak.

FIG. L.—Surface view of blastoderm with a very young primitive streak.

Plate VII.



F. Deighton del.

Plate VII

Plate VIII.

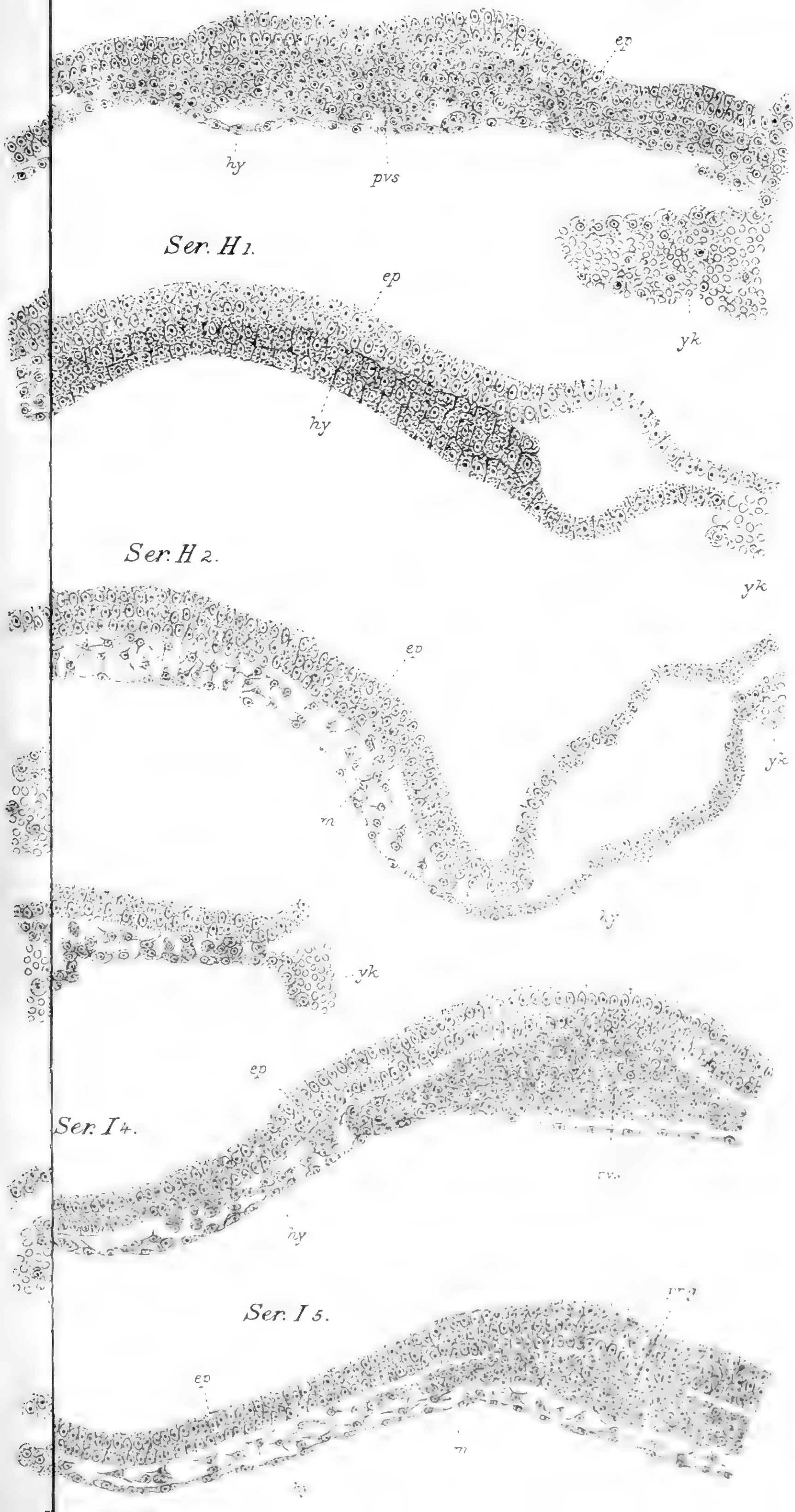
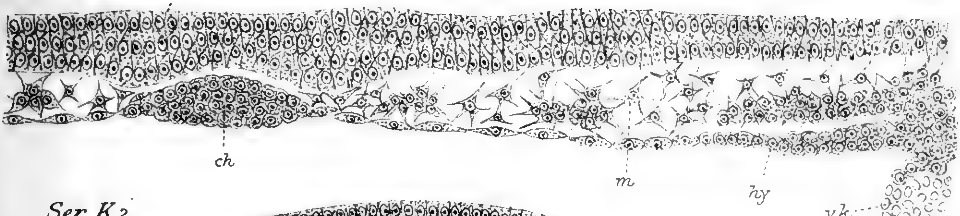

ep
hy
pvs
Ser. H1.
ep
yk
hy
Ser. H2.
yk
ep
yk
m
hy
yk
ep
Ser. I4.
cv
hy
Ser. I5.
ep
m

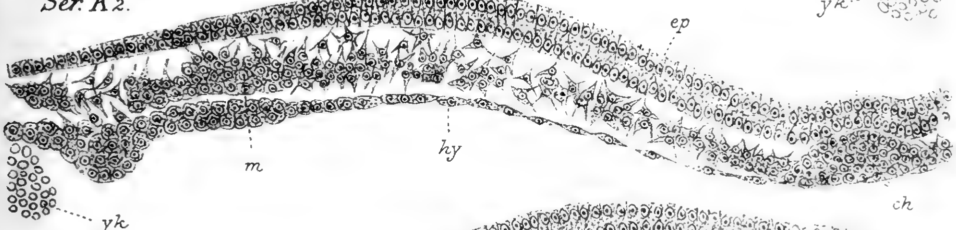
Plate VIII

Plate IX.

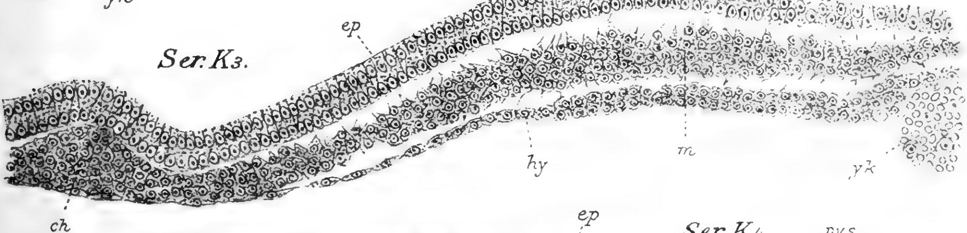
Ser. K1.



Ser. K2.



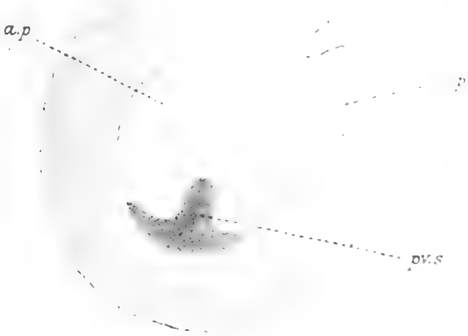
Ser. K3.



Ser. K4.

Ser. K5.

Fig. L.



F. Deighton del.

F. Huth, Lith^r Edin^r

STUDIES

FROM THE

MORPHOLOGICAL LABORATORY

IN THE

UNIVERSITY OF CAMBRIDGE.

EDITED BY

F. M. BALFOUR, M.A., F.R.S.,
FELLOW OF TRINITY COLLEGE, CAMBRIDGE.

WILLIAMS AND NORGATE,
14, HENRIETTA STREET, COVENT GARDEN, LONDON;
AND 20, SOUTH FREDERICK STREET, EDINBURGH.
1880.

S. F. Harmer
with the Editor's kind regards

STUDIES

FROM THE

MORPHOLOGICAL LABORATORY

IN THE

UNIVERSITY OF CAMBRIDGE.

EDITED BY

F. M. BALFOUR, M.A., F.R.S.,
FELLOW OF TRINITY COLLEGE, CAMBRIDGE.

PART II.

WILLIAMS AND NORGATE,
14, HENRIETTA STREET, COVENT GARDEN, LONDON;
AND 20, SOUTH FREDERICK STREET, EDINBURGH.
1882.