Notes on Elasmobranch Development.

By

Adam Sedgwick, M.A., F.R.S.,
Fellow and Lecturer of Trinity College, Cambridge.

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1. On the Formation and Growth of the Elasmobranch Embryo.

My observations on this subject, which were made upon the genera Scylium and Raia, have led me to conclusions which differ in some respects from those of previous observers. In some of the points with regard to the tail I have been anticipated by Schwarz (‘Zeit. f. wiss. Zool.,’ Bd. xlviii, p. 191), Kowalevsky, and Kastschenko (‘Anat. Anzeiger,’ 3); but as Schwarz’s account—excellent though it is—does not go over the whole ground, and Kastschenko’s is without figures, while Kowalevsky’s is inaccessible, being published in Russian, I have thought it worth while to treat the matter fully.

As is well known, the blastoderm attains a certain size before any trace of the embryo is visible, spreading by a uniform growth at all points of its circumference over the yolk. At Balfour’s Stage A, however, the first trace of the embryo appears as a slight thickening at one point of the circumference of the blastoderm. This point is usually regarded as the hind end of the blastoderm. This is not quite correct, for it
really becomes the front end of the future embryo. After the appearance of the embryonic rim the blastoderm still continues to spread over the yolk by a uniform growth of all parts of its circumference, but in the centre of the embryonic rim a slight indentation appears. This indentation shares in the uniform growth of the blastoderm edge, and advances over the yolk equally with the rest of the embryonic rim and general edge of the blastoderm. As the embryonic rim travels away from the point of its first appearance, the surface of the blastoderm so formed—that is to say, the surface of the part of the blastoderm extending between the point of first appearance of the embryonic rim and the embryonic rim at any given moment of its growth—is slightly elevated from the rest of the blastoderm, and traversed by an inconspicuous longitudinal median groove. This raised part of the blastoderm soon becomes marked off by two ridges, which in front, i.e. at the point which marks the site of the first appearance of the embryonic rim, are continuous with one another, while behind they are continuous with the parts of the embryonic rim which bound the indentation. These portions of the embryonic rim are more markedly swollen than the rest, and form the "tail swellings" of Balfour. This elevated part of the blastoderm is the medullary plate, and the shallow groove traversing it marks the line of growth of the indentation above referred to. These points are all illustrated by my fig. 1, which represents the embryo at a stage where the indented embryonic rim has grown back a considerable distance from the point of its first appearance. Various stages in the process may be seen in Balfour’s figures\(^1\) of Stages B, C, D, and in Schwarz’s figs. 1 and 2. The indentation of the embryonic rim is always placed at the hind end of the groove which marks the centre of the medullary plate. This groove is a transitory structure, and soon disappears; its importance consists in the fact that it indicates the line of growth of the indentation of the embryonic rim. (It is conterminous in

\(^1\) ‘Monograph of Development of Elasmobranch Fishes,’ pl. vii; pl. viii of the Memorial Edition.
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extent with the notochord, though the notochord beneath the front part of it is not at first developed.)

It must be clearly understood that the growth of the whole edge of the blastoderm has so far been a uniform one. The indentation in the embryonic rim advances equally (after its first establishment) with the more prominent parts of the embryonic rim called the caudal swellings. There is no reason to suppose that this advance of the indented part of the embryonic rim is due to the fusion of the divergent caudal swellings. On the contrary, there is every reason to suppose that the indented part of the embryonic rim advances by growth of its own substance, just as do the other parts of the edge of the blastoderm.

After a certain time the caudal swellings and the part between them begin to grow more rapidly than the adjacent portions of the edge of the blastoderm, and come to project beyond the latter like a kind of tongue overhanging the yolk (fig. 2). This appears to happen at about the time when the medullary groove is closing in its anterior part to form the medullary canal.

At the same time the edge of the blastoderm remote from the embryo has continued its rapid growth. It is only the edge of the blastoderm next the embryo in which the growth is retarded. The result of this is that the posterior projecting part of the embryo lies in a kind of bay of the edge of the blastoderm. Fig. 2 is drawn from an embryo at a stage when this bay was but little marked.

I now wish the reader to concentrate his attention upon the projecting tongue which will form the under part of the embryo. Its sides, which are part of the edge of the blastoderm, bend ventralwards and towards each other. It consists on its dorsal face of the medullary plate ectoderm, which has become folded so as to form the neural canal (in fig. 2 the neural canal is established in the front part of the embryo, but widely open at the hinder end of this projecting tongue). At

1 A good figure of this is given by His in the 'Zeitschrift f. Anatomie u. Entwick. Gesch.,' 1877, pl. vii, fig. 6.
its edge, which is part of the general edge of the blastoderm, the ectoderm is continuous with the endoderm which forms the under side of the tongue. A good idea of the appearance of a transverse section through this tongue is given by fig. 1 b, pl. x,1 of the ‘Elasmobranch Fishes’ (Mem. Ed.). The hinder end of the tongue is of course notched, and the notch is continued forwards along the line of the groove above mentioned as occupying the centre of the medullary plate, as a slit which actually completely perforates the blastoderm, so as to lead into the space between the endoderm of the tongue and the yolk. This is shown clearly in fig. 3, and at a later stage in fig. 4. Whether this slit is due to a bilobed backward growth of the notched portion of the embryonic rim, the growth at the middle point, i.e. at the bottom of the notch, ceasing—in other words, to an emphasising of the notch already present—or whether it arises as a secondary perforation of the medullary plate and endoderm along the line of the groove before mentioned, I am unable to say; but I think it is due to the former.

While these changes have been taking place—and I must now refer back to fig. 2—the sides of the projecting tongue become bent ventralwards and towards each other until they meet or nearly meet in the ventral middle line. Now two important structural results, which should be noted and understood, follow from this bending: (i) the two angles formed by the junction of the edge of the blastoderm in the embryonic region with the edge of the blastoderm in the non-embryonic region—the angles, one of which is marked a in fig. 2, become closely approximated ventrally beneath the embryo; and (ii) a space is enclosed on the ventral side of the embryo, which space is lined by endoderm, and opens ventrally to the exterior through a slit formed by the contact of the ventrally bent edges of the tongue, and dorsally into the neural canal by the slit in the medullary plate. This space2 is the hind

1 Old edition, pl. ix, fig. 1 b.
2 A section of the tongue in this stage in front of the neurenteric slit is shown in Schwarz’s fig. 16.
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gut, and the two slits which are continuous with one another round the hind end of the embryo are portions of the blastopore. By the time that the two angles marked a and the edges of the embryonic part of the blastoderm have come into contact ventrally, the non-embryonic edges of the blastoderm adjacent to the embryo have grown backwards over the yolk to form the bay mentioned by Balfour. The two sides of this bay, which it will be remembered are portions of the edges of the blastoderm, come to lie close together on the yolk beneath the tail of the embryo. For a little time they remain unfused, and the yolk is still freely exposed between them in a linear streak. This slit, which is bounded by the edges of the non-embryonic part of the blastoderm of the two sides, is a part of the blastopore, and is continuous, passing along the hinder side of what will be called the umbilical stalk, with the portion of the blastopore leading into the hind gut and extending along the ventral side of the tail. This last portion is, as we have seen, continuous with a dorsal portion which leads through the medullary plate into the medullary canal.

The last part of the blastopore to be mentioned is the so-called yolk-blastopore, described by Balfour in the 'Elasmobranch Fishes,' p. 81 (Mem. Edition, vol. iii, p. 296), and in the 'Comparative Embryology,' 1st ed., ch. iii, p. 52. The lips of this portion are continuous with the lips last mentioned as running back on the yolk parallel to one another, and ventral to the tail of the embryo.

To recapitulate: the blastopore of Elasmobranchii is at the present stage—i.e. the stage immediately before closing—an elongated narrow slit, slightly dilated in front, where it lies on the floor of the medullary canal (fig. 3) and more dilated behind (Balfour's yolk-blastopore, 'Comparative Embryology,' vol. ii, ch. iii, fig. 30 b). Between these two limits it takes the course of a reversed letter S, as shown in the adjoining woodcut, where its lips are represented unfused.

The anterior part, a b, perforates the floor of the medullary

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1 Again see Schwarz's fig. 16, d.e.
canal, and is dorsal; this is continuous round the end of the
tail, \( bc \), with a ventral part, which extends forwards along the
ventral side of the tail, \( cd \), as far as the yolk-stalk, along which
it passes, \( de \), to continue backwards along the yolk, \( ef \), as the
slit-like non-embryonic part of the blastopore, which passes
behind into the more dilated and posterior part of the so-called
yolk-blastopore.

Shortly after this stage the blastopore completely closes,
excepting one point in its dorsal portion, which persists for
some time as the neurenteric canal.

Balfour, as is well known, was the first to compare the primi-
tive streak of the Amniota to "the linear streak in Elasmo-
branchii, formed by the coalesced edges of the blastoderm
which connect the hinder end of the embryo with the still
open yolk-blastopore" ("Comparative Embryology," 1st ed.,
vol. ii, ch. xi, p. 240); and he also says, in the same place,
that "the passage at the front end of the primitive streak [the
neurenteric canal] is the dorsal part of the blastopore, which
in Elasmobranchii becomes converted into the neurenteric
canal." But he never, either in the chapter quoted or in
his account of the actual development of Elasmobranchs in
ch. iii, p. 52, describes the ventral embryonic part of the
blastopore (woodcut, \( cd \)) which connects together the linear
streak on the yolk, \( ef \), with the dorsal part of the blastopore, \( ab \).

In fact, he says (ch. iii, p. 52), "It is interesting to notice that,
owing to the large size of the yolk in Elasmobranchs, the pos-
terior part of the primitive blastopore becomes encircled by
the medullary folds and tail swellings, and is so closed long

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2 This part of the blastopore is clearly recognised and figured by Schwarz.
before the anterior [what I have called posterior] and more ventral part, which is represented by the uncovered portion of the yolk."

I have dwelt at some length upon this point because Balfour's description of the Elasmobranch blastopore has always bothered me, in that it does not show the connection between the yolk part of the blastopore—the linear streak—with the dorsal part; and also because I wish to present a slight modification of the comparison which Balfour made between the primitive streak of the Amniota and the linear streak on the Elasmobranch yolk. Balfour does not say that the two structures are homologous; he expressly guards himself from this. He says ("Comparative Embryology," 1st ed., vol. ii, ch. iii, p. 51), "A linear streak [my woodcut, ef] formed by the coalesced edges of the blastoderm is left connecting the embryo with the edge of the blastoderm. This streak is probably analogous to (though not genetically related with) the primitive streak in the Amniota" (the italics are mine). But he undoubtedly does compare the primitive streak with this linear part of the yolk-blastopore of Elasmobranchs; and he says ("Comparative Embryology," vol. ii, 1st ed., ch. xi, p. 240), "That it (primitive streak) is in later stages not continued to the edge of the blastoderm, as in Elasmobranchii, is due to its being a rudimentary organ."

The modification which I would propose to suggest in the comparison is as follows. The primitive streak of the Amniota is, as is well known, partly involved in the tail fold, and tucked under on to the ventral surface of the embryo. It thus becomes divided into a dorsal part, at the front end of which is the neurenteric canal or its rudiment, and a ventral part. The dorsal part is in birds for some time placed in a dilated posterior part of the still open medullary groove called the sinus rhomboidalis. This part I would compare to the dorsal part of the blastopore shown in the same position and relations in my figs. 3 and 4. The ventral part, on the other hand, I would compare to the part of the blastopore which in Elasmobranchs runs along the ventral side of the tail
to the yolk-stalk (my woodcut, c d); while the linear part of the yolk-blastopore in Elasmobranchii (my woodcut, e f) is unrepresented or rudimentary in Aves and Amniota generally—is, in fact, the rudimentary part referred to by Balfour in the above quotation from the 'Comparative Embryology.'

The comparison has the advantage of bringing together the growing points of the embryos in the two cases. In Amniota the primitive streak is the growing point where the cells are proliferated, out of which the greater part of the embryo is formed. In Elasmobranchii the tail swellings which form the sides of the dorsal and ventral parts of the embryonic blastopore (my woodcut, a b c d) are the points where the active growth takes place, as a result of which the hinder part of the embryo is formed. Indeed, the prominence of the tail swelling is due to the mass of mesoderm-cells produced by this proliferation at the edge of this part of the blastopore.

The proliferation of mesoderm takes place in a rudimentary fashion in Elasmobranchii, at all points of the circumference of the blastoderm; which circumference, gradually creeping over the yolk and enclosing it, constitutes the lips of the widely open blastopore; but the proliferation is very feeble except at the notched embryonic rim, the growth of which forms, as above described, the tail end of the embryo.

It is interesting to notice the different manner in which the tails of Elasmobranchii and Amniota are formed. There is in the former no tail fold as in the latter, but simply a bilateral bending round of the posterior tongue-like projection formed by the growth backwards of the notched part of the embryonic rim.

The above account of the Elasmobranch blastopore is not given for the first time, although when I did my work—now some years ago—I was unaware that a correct account of the process had been published by Schwarz in 1889 ('Zeit. f. wiss. Zool.,' Bd. xlviii).

Kastschenko, in the previous year, published an excellent paper on Selachian development in the 'Anatomischer An-
zeiger,' vol. iii, p. 445, in which he calls attention to the fact that Kowalevsky, in a paper published in Russian in about 1870, was the first to describe it correctly. That Kowalevsky's description, if correct, as maintained by Kastschenko, should have been overlooked, is of course attributable to the fact of its being written in Russian, and not reproduced in any of the more commonly known European languages. It seems a great pity that an observer of the eminence of Kowalevsky should thus secrete his work and render it unavailable to science.

Kastschenko's account of the matter is as follows:

"The closure of the medullary tube presents in the dogfishes interesting peculiarities, which were first discovered and correctly described by A. Kowalevsky. . . . . The medullary folds are continuous at their hinder ends with the caudal lobes, and by means of the latter with the general edge of the blastoderm. Each caudal lobe presents a marked knee-shaped bend, the point of which is directed backwards. The lateral limbs of the paired caudal lobes approach one another on the ventral side of the embryo; and when the medullary folds fuse on the dorsal surface the adjacent caudal lobes also fuse. By the fusion of the former the medullary tube is formed, and by the fusion of the latter the neurenteric canal and the hind gut. The hind gut, therefore, is the immediate continuation of the medullary tube, and the neurenteric canal must be regarded as nothing else than a portion of the blastopore. Further forwards the hind gut remains for some time open ventrally, but eventually this opening also fuses, the anus appearing considerably later in the same place."

This account, however, as will be gathered from my description, does not give the whole gist of the matter. It fails to notice the slit-like form of the dorsal part of the blastopore which perforates the floor of the medullary canal, and the author does not appear to understand, or at any rate fails to draw attention to the fact that the ventral opening leading into the hind gut is part of the blastopore, and is continuous with the slit-like non-embryonic part of the blastopore running along the yolk. The only point in which it supplements
Balfour's description is in the account given of the formation and of the at first open condition of the hind gut.

I quite agree with Kastschenko's remarks on the view that the embryo is formed by the fusion of two separate halves. It must, however, be admitted that the embryo is formed by a bilateral growth; that there are two growing points—one in each caudal lobe, which contributes to its development. With regard to the growth of the blastoderm, I agree essentially with Balfour, but I differ from him as to the growth of the embryo. His views are expressed in the following passage ('Comp. Emb.,' 1st ed., ch. iii, p. 35; Mem. Ed., vol. iii, p. 43) :—"This rim [the embryonic rim] is a very important structure, since it represents the dorsal portion of the lip of the blastopore of Amphioxus. The space between it and the yolk represents the commencing mesenteron, of which the hypoblast on the under side of the lip is the dorsal wall. The ventral wall of the mesenteron is at first formed solely of yolk, held together by a protoplasmic network with numerous nuclei. The cavity under the lip becomes rapidly larger, owing to the continuous conversion of lower layer cells into columnar hypoblast along an axial line passing from the middle of the embryonic rim towards the centre of the blastoderm." The italics are mine, and are used to bring out the point in which my view is divergent from Balfour's. He regards the embryonic rim, at its first appearance, as marking the hind end of the future embryo, which is formed by a differentiation forwards of the blastoderm, as already established. I, on the other hand, regard the same point as marking the extreme front end of the future animal, and consider that the notched embryonic rim grows over the yolk uniformly with the rest of the blastoderm edge. It certainly does so extend itself, at any rate until the stage of my fig. 1, and of fig. 2 also, allowing for the shoot back of the caudal tongue. And it appears to me that this view—which is, to a certain extent, in accordance with the view of Roux on the growth of the Amphibian embryo ('Anat. Anzeiger,' vol. iii, p. 705)—must be looked upon as being nearer the
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truth than Balfour's; for if Balfour's view is correct, the embryonic rim being stationary in growth backwards—all the differentiation being forward—ought, from the first, to be placed in a bay of the edge of the blastoderm.

According to my view, then, the blastoderm grows uniformly over the yolk at all points of its circumference. Indeed, its edge is everywhere raised into a marked ridge, which is continuous with the embryonic rim. The difference between the growth at the embryonic rim and elsewhere consists in the fact that, as the former extends over the yolk, a trail of columnar epithelial cells is left separated from the yolk by a space, whereas elsewhere the raised edge of the blastoderm simply slides over the yolk, leaving, as far as one can see, little (possibly a few mesoderm-cells) or no trail.

Further, it is clear, from what I have said above, that the notch of the embryonic rim represents the anterior end of the blastopore, and that on the view of embryonic growth above stated the blastopore does at one time or another perforate the whole length of the medullary plate. Posteriorly it does actually form for a short time a slit through the medullary plate, but anteriorly it keeps closing up as the embryonic rim grows backwards, so that it is never present in this region as more than a notch.

It will be maintained by some that this view of the growth of the embryo, and of the relation of the blastopore to the medullary plate, is incompatible with the objection to the concrescence theory above formulated. To this the reply would be that the body of the Elasmobranch embryo is no more formed by the fusion of two lateral halves than is the body of the Peripatus embryo, in which nearly the whole of the ventral surface is at one time traversed by the long blastopore.

The phenomenon we are in both these cases dealing with is the closure of the blastopore; and to talk about concrescence and fusion of two halves is merely obscuring the real question, and seeking to explain a process of growth by a phrase which has no satisfactory meaning.

Before leaving this part of my subject I may point out that...
while the anus is formed within the area of the blastopore, and is in some Vertebrates actually a persistent part of the blastopore, in no Vertebrate has the mouth been traced into connection with the blastopore. The fact that no such connection has been established is not surprising when one remembers how early the anterior part of the blastopore closes in Elasmobranchs and Amphibia, and must not be taken as proving that the blastopore never extended in front of the present medullary plate on to the ventral surface of the head. I shall return to this question in the part of this paper which deals with the Vertebrate head.

It will be seen from the above account that the behaviour of the blastopore of Elasmobranchs—in its relation to the anus, neurenteric canal, and growing point—resembles very closely that of the frog as described in the admirable paper by Asheton and Robinson in vol. xxxii of the 'Quarterly Journal of Microscopical Science.'

2. On the Formation of the Mouth and Gill-clefts in Elasmobranchs.

I have had a number of drawings made of the head of embryos of Scyllium canicula to illustrate certain points in the formation of the mouth and clefts. Some of the points have been known before, and some are, I believe, recorded for the first time.

The mouth makes its first appearance in Stage I as a row of dots lying in the middle line between the two mandibular arches (fig. 5), and connected by a kind of shallow groove in the ectoderm, along which the ectoderm and endoderm are fused. These pores soon become connected (fig. 6) to form a long slit, which extends from the ventral point of junction of the mandibular arches forward along the depression between the latter as far as the pocket of ectoderm which is destined to give rise to the pituitary body. The first rudiment of the mouth actually extends into the rudiment of the pituitary body. At the front end of the buccal slit the fore-gut, the notochord, the ectoderm, and the mesoderm are all con-
The mouth soon widens and shortens (figs. 8, 10, 12) until it attains its adult form.

The mandibular arch is at first directed almost from before backwards (figs. 5, 6, 7), and its anterior end is under the mid-brain.

The hyoid arch is also directed very much backwards, though not so much as the mandibular; and its anterior (dorsal) end is well in front of the auditory sac (fig. 7).

The branchial arches are also directed backwards, but the inclination is less in the posterior arches than in the anterior (fig. 9).

The question now arises, what is the meaning of this backward direction of the visceral arches? The only answer that I can suggest to this question is that the same cause which has produced the flexure of the brain, and of the front end of the notochord, has affected the arches. If this is so the cranial flexure should really be called cephalic flexure, for it affects not merely the brain, but all the organs of the head.

To account for this flexure we must either suppose that there has been a great forward extension of the dorsal anterior end of the head, which would carry the dorsal ends of the arches forward, and, if the anterior end of the notochord and the infundibulum, i.e. the anterior end of the cranial axis, remained fixed at the front end of the mouth, would also cause the flexure of the brain and anterior part of the notochord; or that there has been a great shrinking of the ventral parts of the head just behind the mouth. If either of these views is correct, it necessarily follows that the mouth was originally a nearly vertically directed slit looking straight forward. It may even have extended on to the dorsal surface.

The early slit-like form of the mouth is very remarkable, and may be regarded as being in favour of the view that the mouth is derived from the anterior part of the slit-like blastopore, though I admit that this does not constitute a very powerful argument.

The extension forward of the first rudiment of the mouth into the pituitary pocket is also very remarkable.
In Scyllium and Raja the hyobranchial cleft is formed before the spiracular cleft.

It is interesting to notice in this series of heads the manner in which the at first straight mandibular arch is bent upon itself at the point which will become the point of articulation of the upper and lower jaws. The part anterior to the angle develops a forward projection and forms the upper jaw—the part behind is bent ventrally and outwards and forms the lower jaw. The widening and shortening of the mouth seems largely due to this bending of the mandibular arch (cf. series of figures of heads in ventral and side view).

The view that the mouth is derived from the anterior end of the blastopore was originally put forward in my paper on "The Origin of Metameric Segmentation" ('Quart. Journ. Micr. Sci.', 1884). Considering the early stage at which the anterior end of the blastopore closes in Vertebrates, and the relatively late appearance of the mouth, one would not expect to find any direct embryological evidence in support of this view. For the argument and indirect evidence in favour of it I refer the reader to pp. 73 et seq. of my paper above mentioned. To that evidence I now add the long slit-like form of the primitive Elasmobranch mouth.


V. Wyhe describes the cranial mesoderm in Scyllium as segmenting from behind forwards, and he says that in Stage I—and not before—the whole of the cephalic mesoderm is broken up into somites, and that all these somites contain a cavity except the first.

Kastschenko says that the first somite is formed at what appears to be the junction of the head and trunk, and that the segmentation of the mesoderm extends backwards and forwards from this point. Anteriorly it becomes more and more

indistinct as the front end of the embryo is approached, so that the anterior part of the cephalic mesoderm is at no stage of development broken up into somites. This unsegmented part of the cephalic mesoderm, which corresponds, according to Kastschenko, to several somites, is comprised in the second somite of Wyhe. The first somite of Wyhe occupies, in Kastschenko's opinion, a special position. Kastschenko's observations were made on the genera Scyllium and Pristiurus, but he does not state precisely the ages of the embryos to which his observations refer, nor distinguish between the genera in describing his observations. As the different genera of Elasmobranchs differ, as I hope to show, very remarkably in the condition of the mesoderm and during these early stages, this latter point is one of considerable importance.

It is perfectly obvious to anyone who examines Elasmobranch development that the work of these two observers has been exceptionally thoroughly and carefully done; and if the results and views which I have arrived at differ from theirs, I would wish my work to be considered alongside of theirs, not as contradicting, but as supplementing it, by the future workers who succeed in obtaining a fuller and more accurate knowledge of the development of the different genera of this interesting group.

Balfour ('Elasmobranch Fishes,' Mem. Ed., p. 302), in describing Pristiurus, says that "coincidently with the appearance of a differentiation into a somatic and splanchnic layer the mesoblast plates become partially split by a series of transverse lines into protovertebræ." This statement I can entirely confirm for Pristiurus and Scyllium; its importance has not been fully appreciated or understood. What it means is this, that the body-cavity at the very first sign of its appearance (differentiation of mesoderm into somatic and splanchnic layers) is segmented.

Balfour goes on to say, "In the head, so far as I have yet been able to observe, the mesoblastic plates do not at this stage (D) become divided into protovertebræ." The term head
here must be regarded as meaning the anterior end of the body, for it is not possible in these young embryos to distinguish the head from the trunk. I am, however, in entire agreement with the statement that there is a stage in which there is a considerable tract of mesoderm in front of the first formed somite, which is entirely unsegmented, and with no signs of differentiation into somatic and splanchnic layers. But in Pristurus this stage is of very short duration, for, according to Balfour, even in Stage D there is a cavity in the anterior part of the mesoderm. I can entirely confirm Balfour as to the presence of this cavity at this early age in Pristurus; but it is not, as he seems to imply, ever continuous with the general body-cavity. It is, indeed, a somite—the second or mandibular somite of v. Wyhe,—and its appearance is followed by the breaking up of the mesoderm between it and the first so-called trunk somite into successive and contiguous but indistinct somites. I am not able to say in what order these somites are formed, whether from behind forwards, as Kastschenko maintains, or in the reverse direction. All I can say on this subject is that in Pristurus the mandibular somite is formed before those behind it, and that in Scyllium I have an embryo a little older than Stage F, but younger considerably than Stage G, in which the whole of the mesoderm in front of the first so-called trunk somite is broken up into somites successively traceable in a series of transverse sections. The first of these somites (the second of Wyhe) is the most distinct and, I expect, the first formed, as in Pristurus.

This early segmentation of the anterior part of the mesoderm into somites almost exactly like those in the hinder part of the body is a morphological point of great interest. It is very transitory in the genera mentioned, and disappears before any trace of the pharyngeal pouches are formed, except in the case of the mandibular somite, and possibly also of the one next it. In Stage I, where, according to v. Wyhe, the segmentation of the anterior part of the mesoderm is complete, I cannot find in either Scyllium or Pristurus or Raja any of the somites described by him as the fourth, fifth, and sixth;
moreover the posterior limits of the third cannot be made out in Stage I.

Dohrn, however, in his fifteenth study describes a complete mesodermal segmentation as occurring in *Torpedo marmorata* at a stage in which the mandibular and hyobranchial pouches could be made out. The embryos in question were considerably younger than the embryos in which v. Wyhe first observed the segmentation of the cranial mesoderm, and Dohrn ascribes them to Stage F; but the above pouches being present, he was able to compare his cephalic myotomes with those of Wyhe. He makes out ten myotomes in front of the hyoid pouch, arranged as follows:

- 4 myotomes in the place of Wyhe's first.
- 3 " " " second or mandibular.
- 3 " " " hyoid.
- 2 or 3 " " " fourth.

He admits that they are very transitory structures, and that they have lost their distinctness (by fusion with one another) in Stage G, i.e. before the stage at which v. Wyhe first saw them. Having a very practical acquaintance with the great variation of the mesoderm in embryos of different genera of Elasmobranchs I do not venture to impugn the accuracy of Dohrn's observations on a genus which I have not examined; but knowing the extreme difficulty of satisfactorily observing these rudimentary cranial somites, even when they are undoubtedly present, I cannot help feeling that it is desirable that Dohrn's statements should receive some confirmation. This confirmation is, to a certain extent, supplied by Herr Killian's recently published work on *Torpedo ocellata*. I say "to a certain extent," because Killian's list of somites does differ slightly from that of Dohrn. I think that it is possible, and I trust that Dr. Dohrn (and Herr Killian) will forgive me for making the suggestion, that he has been misled by deceptive appearances afforded by the somites at the time of their disappearance. I know very well that in looking

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2 'Anat. Anzeiger,' Ergänzungsheft, 1891.
through any one series of sections it is very easy to make out what appears to be a great number of somites, but on carefully comparing the two sides of the embryo, and on estimating the intervals which the somites occupy, it is in my experience always found (after Stage F in the head region) that, with the exception of the first three head segments and the three posterior segments, these supposed somites are in embryos, in which the rudiments of the spiracle and hyoid cleft are apparent, quite irregular, and are either simply spaces in the mesoderm or remains of broken-down somites. This result comes out still more forcibly if one attempts to confirm one's observations on one embryo by similar observations on another embryo of the same size.

But even if Dohrn is right in his enumeration of the anterior somites, it is clear that Torpedo differs much from Scyllium, Raja, and Pristiurus, whether my account or Wyhe's be taken as correct. For in Torpedo there are four somites where in the other genera there is most unquestionably one, e.g. the somite of Wyhe.¹

It would appear, then, that if the number of primitive cranial somites in any given region of the head does really differ in closely allied genera in the manner indicated by the divergent observations of Wyhe, Dohrn, Killian, and myself, the supposed indications of segmentation which are found in the adult, and are constant throughout the Vertebrata, can have very little value as real tests of the primitive metameric segmentation—of the segmentation which obviously persists in the trunk region, and which begins with the segmentation of the mesoderm, and is moulded upon it in the manner characteristic of all metamereic segmented animals.

We may, I think, even go further, and say that the adult arrangements of nerves and branchial arches, &c., characteristic of the Vertebrate head, must have arisen subsequently to

¹ I leave out of consideration the supposed somite anterior to the premandibular somite (first of Wyhe), which has been described by some observers in Acanthias, Torpedo, &c. I have seen traces of it in Scyllium, but it is in that genus merely a diverticulum of the premandibular somite.
the disappearance of the primitive segmentation. This position will be still further strengthened if my contention turns out to be correct, viz. that in embryonic development the mesodermal cranial segments do largely become indistinguishable before the adult landmarks have appeared.

If my arguments and facts are sound, it follows that any attempt to elucidate the structure of the adult head from the point of view of its being composed of a series of segments comparable to those of the trunk is doomed to failure; and the result of the whole inquiry shows up most thoroughly the weakness of the position of those who hold embryological research to be of small importance in comparison with the study of adult structure.

To a student of the multitudinous changes of structure which an organism passes through in the course of its existence it seems strange even now, and in the future will ever seem stranger to the philosophical morphologist, that one condition of structure only, and that the most complex and inexplicable, should have been regarded by anyone as holding the key to the solution of even a simple anatomical problem.

To sum up the matter, v. Wyhe holds that there are nine cranial segments which can be traced into the adult. Dohrn holds that there is a much greater number of cranial somites, some of which can be traced into the adult, and some of which disappear. I agree with Dohrn in asserting that the anterior mesoderm is completely segmented in Stage F, but maintain, in opposition to him, that it is not possible to say how these segments are related to adult structures, because they have for the most part vanished before any of the adult landmarks have appeared.

The premandibular somite of Balfour (the first somite of Wyhe).—There can be no doubt this is not, as Balfour supposed, separated off from the mandibular.

Kastschenko says that it develops from what he calls the prechordal portion of the gut, which becomes solid when the medullary plate is formed, and then subsequently again acquires a cavity. I find myself unable to accept this account
of the origin of the first somite. It is true that at the time of the formation of the medullary plate the notochord stops some little distance short of the front end of the body, and there is a portion of the gut in front of it; but this is only a temporary state of affairs, and is due to the fact that the front end of the notochord, which is developed from behind forwards, is not yet formed: moreover the solid mass of endoderm referred to by Kastschenko is present at the front end of the gut even at this stage. When the notochord has acquired its furthest anterior extension in Scylium, just before Stage G, it terminates in a solid mass of cells, which is continuous also with the front end of the gut. The notochord has hitherto during the whole of its growth been continuous in front with the endoderm, and its condition at the period referred to is merely a persistence of that continuity. Wyhe's account of the anterior end of the notochord appears to me to be quite correct.

When the notochord has acquired its utmost anterior extension there is no portion of the gut in front of it, but merely this solid mass of cells, with which both it and the gut, and afterwards the ectoderm of the buccal slit and pituitary body, are continuous, and which underlies the very front end of the medullary tube. If this mass of cells be regarded as partly consisting of the anterior end of the notochord still undifferentiated, it may be said that the notochord reaches in Scylium, at any rate, to the very front end of the neural tube; in other words, that Scylium at this stage is truly cephalochordate in the sense that Amphioxus is cephalochordate.

The solid mass of cells in which the notochord and gut terminate becomes in Scylium and Pristiurus very early, before Stage G, connected with the ventral ectoderm. Wyhe, who connects this fusion with the formation of the mouth, puts it down as taking place later in Stage H; but I can positively assert that in Scylium and Pristiurus it is present before Stage G—before any trace of the cranial flexure has appeared.
There can be no question that the first or preoral somite develops in connection with this solid mass of cells, but whether entirely from it, as Wyhe appears to maintain, or only partly from it, is difficult to say. In Scyllium there are very clear indications that a part of the tissue from which the somite develops is derived from a paired ingrowth from the ectoderm. In Stage G the cell mass is continued forwards on each side in continuity with the ectoderm, and these paired tracts present the appearance of ingrowths.

The mass of cells of which I am speaking presents very remarkable differences in its relation to adjacent organs in the different genera that I have examined. In Scyllium and Pristurus it is continuous with the ventral ectoderm throughout its whole extent from the earliest stage at which I have seen it, i.e. Stage F, or the earliest stage at which the ventral ectoderm is folded in.

In Scyllium it is for the most part not continuous with the medullary ectoderm, unless there is such a continuity, of which I am not certain, at its very front end. In Pristurus and Raja it is markedly continuous with the medullary ectoderm throughout its entire extent, while in Raja the dorsal lateral outgrowths, which are soon formed from it, are also continuous with the medullary ectoderm. Further, Raja differs from the other two genera in that this cell-mass is not continuous with the ventral ectoderm at all (excepting through the endoderm and buccal slits).

As Wyhe has correctly stated, the first or premandibular somite of Balfour is formed by the hollowing out of this mass of cells and its lateral prolongations, and Kastschenko seems to be justified in placing it in a different category from the other somites. It differs from the other somites in two respects: (1) in its connection at origin with the ectoderm, either of the body-wall or of the neural tube (Raja, Pristurus); (2) in its continuity with its fellow across the middle line.

Before leaving this cell mass which gives rise to the first somite, and which eventually breaks off from the various...
organs with which it is at first continuous, i.e. notochord, ectoderm, and gut, I should like to point out a resemblance in its early condition to the primitive streak of the Amniota. Like the primitive streak, it is a densely packed mass of nuclei in continuity with all the layers and organs of the body. The ectoderm, endoderm, notochord, and mesoderm, all are continuous with it; and as the primitive streak is the growing point for the hind end of the embryo, so it appears to contribute in a similar manner to the front end.

The Anterior Somites in Raja.—In Raja the segmentation of the anterior mesoderm and the prominence of the first two somites are not nearly so conspicuous as in the other genera. The condition of the anterior mesoderm after its separation from the endoderm is quite different from that in Scyllium and Pristurus. It does not assume the condition of an “epithelium” arranged round the cavities or the incipient cavities of somites. On the contrary, it at once assumes the form of “embryonic connective tissue,” i.e. of a mass of stellate cells all connected together by their processes. In other words, it at once takes on the form which is only secondarily attained by the same mesoderm of the two other genera after passing through the epithelial condition. This difference in the early structure of the cephalic mesoderm of Raja and Scyllium is another proof, if such were needed, that the distinction between “mesenchyme” and epithelial mesoderm to which the Hertwigs have so prominently called attention has not the importance which they attribute to it. The cavities of the first two somites make their appearance in this stellate mesoderm at about Stages G, H. But they are at first inconspicuous, having the appearance of blood-vessels, and are without the conspicuous epithelial lining. In fact, the cells lining them have at first simply the characters of the reticulate mesoderm tissue, of which, indeed, they are merely a part.
CONTINUITY OF CELLS AND LAYERS.

The continuity between the different layers and organs of the embryo to which I first called attention in Peripatus is found in all Vertebrate embryos that I have examined. In fact, there is a network of pale protoplasmic fibres extending inwards from the nucleated protoplasm of the various surfaces. When this network has nuclei at the nodes, we get the reticulated tissue, or embryonic mesoderm, or mesenchyme. In Scylium it is at first sparse and without nuclei. In Raja, on the other hand, it is very richly developed, and rich in nuclei. In Raja, in other words, the protoplasmic connections passing between the various organs and layers are very conspicuous and well marked. In Scylium this tissue is at first without nuclei, as I have said. But soon it acquires nuclei and becomes denser. Where do the nuclei come from? In my opinion they are derived partly from the epithelial walls of the somites, partly from the anterior mass of mesoderm in which the notochord, gut, &c., ends, and partly from the growing tissue of the caudal swellings, and perhaps also from the neural crest.

We now pass on to speak of the neural crest in those Elasmobranchs which I have studied.

The nerve crest was first discovered by Balfour in the trunk region of Elasmobranch embryos. Marshall has observed it in the chick, and describes it as occurring in the anterior part of the spinal cord region and extending continuously forward into the fore-brain.

Van Wyhe and Kastschenko also both describe the nerve crest in the Elasmobranch embryos they examined as reaching from the region of the fore-brain continuously backwards. The cranial nerves and the posterior roots of the spinal nerves grow out from the nerve crest, and the nerve crest persists itself in part as the longitudinal commissure. Both Balfour and Marshall state that this longitudinal commissure extends

back continuously from the root of the glossopharyngeal to
the spinal cord, connecting together the posterior spinal roots
and the roots of the vagus and glossopharyngeal. It is not,
however, developed in front of the glossopharyngeal, the nerve
crest atrophying between the ninth and seventh, and between
the seventh and fifth nerves.

My observations agree with this account except in one
point, and that relates to the nerve crest. In Scyllium and
Pristiurus the nerve crest is not a continuous structure, as
Wyhe and Katschenko assert (Balfour and Marshall have no
observations on the cranial part of the nerve crest in Elasmo-
branchs). It is in three separate pieces. The first of these
is found in the anterior part of the brain; the fifth nerve and
presumably the opthalmicus profundus grow out from it. The
second is found a little further back, and gives origin to
the seventh and eighth nerves. The third piece occurs a little
further back, and reaches from the hind brain continuously
back the whole length of the spinal cord. The ninth and
tenth cranial nerves and the posterior roots of all the spinal
nerves grow out from it. It is this latter part of the nerve
crest which gives rise to the longitudinal commissure of
Balfour.

There are three views as to the origin of the peripheral
nerves.

1. According to Hensen’s view, the rudiments of the nerve-
fibres are present from the beginning as persistent remains of
the primitive connections between the incompletely separated
cells of the segmented ovum.

2. Balfour regarded them as cellular outgrowths from the
central nervous system extending to the periphery. The
original continuity between the central and peripheral organs,
which must have existed, has, it was supposed, been lost in
ontogeny by rupture, and reacquired by means of these out-
growths.

1 ‘Virchow’s Archiv,’ vol. xxxi, 1864.
3. The view of His, which was previously held by Bidder. According to this view the nerve-fibres are the elongated processes of cells. The anterior roots are derived from non-cellular outgrowths of the spinal cord, consisting of the elongated processes of the nerve-cells of the central organ. The fibres of the posterior roots, on the other hand, are the elongated processes of the ganglion-cells of the ganglion on the posterior roots. Processes of these cells grow out to the periphery and inwards to the centre.

Balfour expressed on a priori grounds a strong preference for the view of Hensen, but rejected it on the ground that there was no evidence for the connection which it demanded. Now, however, we know that in many types the segmentation of the ovum does not bring about a complete separation of the cells of the ovum. 2

There is no such separation in Peripatus; and in many Arthropoda—if not in all—it is known not to take place. It does not take place in Elasmobranchs, as I can certify from my own observations; but for a summary of the facts and a discussion of the whole question I must refer the reader to my monograph already quoted. 3

If the segmentation of the ovum does not bring about a complete separation of the cells of the germ, as it was formerly supposed to do, then the connections required by Hensen's theory exist.

Turning to the special case before us of the Vertebrata, I have in the present paper dwelt upon the fact (see above, p. 581) that the cells of the young embryo (subsequent to cleavage) are connected by delicate processes, and that these processes are often extremely fine, and unite together into networks below the epithelial arrangement of the protoplasm which is characteristic of the surfaces. This network is sometimes of a very

1 'Anatomischer Anzeiger,' vol. iii, p. 500.
loose mesh, and its fibres are always delicate; and it is no

doubt often torn and destroyed by the preserving processes to

which the embryo has to be subjected. But delicate as it is,
there can be no doubt of its existence in Vertebrate embryos;
and there can be no reasonable doubt that it is derived from
the processes and strands left between the cells as a result of
the incomplete cleavage of the ovum. There can be no doubt,
I say, that the network exists; but that the peripheral nerve-
fibres and the central nerve-fibres are derived from it has not
yet been shown. That is the point which now needs investi-
gation, and I hope myself to treat of it in a future paper.

Meanwhile I may say that there is in my opinion evidence
to show that the whole of the nervous connections (by nerve-
fibres and otherwise), both in the central organ and at the
periphery, are developments of this pre-existing network, which
connects together at all times the whole of the cells derived
from the fertilised ovum.

I do not dispute for one moment the description given by
Dohrn\(^1\) of the structure of particular stages in the development
of a nerve-fibre; but in saying that it consists of a row of ecto-
derm-cells laid on end to end he is, I think, going beyond his
facts, being led to such an interpretation of the appearances
not so much by observation of previous stages as by a process
of reasoning based upon the cell theory of structure, which
theory implies that the animal body at one stage of its onto-
geny consisted of cells which are separate from one another
and only secondarily fuse to form the adult tissues and com-
binations.

\(^1\) 'Studien z. Urg. d. Wirbelthierkörpers,' No. 17.
NOTES ON ELASMOBRANCH DEVELOPMENT.

EXPLANATION OF PLATE XXXV,

Illustrating Mr. Sedgwick's "Notes on Elasmobranch Development."

Fig. 1.—Embryo of Scyllium canicula, 2½ mm. in length. The hinder end of the embryo is notched. The medullary groove is just beginning. The tail swellings of Balfour are well marked.

Fig. 2.—Embryo of Raja ? sp., 4 mm. in length. The medullary groove is closed except at the hind end. The notched embryonic part of the edge of the blastoderm has grown faster than the rest, and come to project over the surface of the yolk. The sides of this projection are already slightly bent ventrally. They will eventually meet and form the ventral part of the caudal region of the body.

Fig. 3.—Raja ? sp. Embryo of Stage E or F, 4½—5 mm. in length. The medullary canal is still open, but the medullary folds are almost touching except behind, where the medullary canal widens out in a wide medullary groove, in the floor of which is placed the dorsal part of the blastopore. The blastopore is slit-like, but dilated in front; posteriorly it is continued round the hind end of the body into the ventral portion.

Fig. 4.—Raja ? sp. Stage E or F, 5—5½ mm. in length, a little older than Fig. 3. Medullary canal closed except behind, where it widens out and encloses the blastopore. The blastopore is slit-like, but the hinder end of the dorsal portion is faintly marked.

Figs. 3 and 4 are somewhat diagrammatic, but they show correctly the relations of the medullary groove and dorsal part of the blastopore. I hope to publish figures of the sections through them shortly.

Fig. 5.—Ventral view of head of Scyllium canicula between Stage I and X. Total length 7—8 mm. The two first pharyngeal clefts are open. The mouth rudiment is present as a longitudinal groove in the ectoderm of the buccal depression, which is fused with the endoderm. At intervals there are perforations along this groove. The groove reaches into the rudiment of the pituitary body. The mandibular arch is present as a backwardly directed longitudinal ridge, and bounds the buccal depression externally.

Fig. 6.—Ventral view of head of Scyllium canicula a little older than the preceding. The buccal groove has become a longitudinal slit.

Fig. 7.—Side view of head of Scyllium canicula a little younger than Stage X. Total length about 9 mm. I could not distinguish any trace of...
the limbs. I do not think the fourth slit is open. The posterior end of the mandibular arch is slightly bent ventralwards.

Fig. 8.—Ventral view of head of same embryo drawn to a slightly smaller scale. The anterior part of the buccal slit has become much wider.

Fig. 9.—Side view of head of Scyllium canicula about Balfour’s Stage K. Total length about 11—12 mm. External gills have appeared on the first and second branchial arches. The ventral bend of the hind end of the mandibular arch is more marked.

Fig. 10.—Ventral view of the same head drawn to a slightly smaller scale. The future angle of the jaw can be distinguished, the mouth being widest at that point. The posterior slit-like part of the mouth is still present.

Fig. 11.—Side view of head of Scyllium canicula about Balfour’s Stage L. Total length about 16 mm. The external gills have increased in number, and are present on the mandibular arch. The angle of the jaw where the lower part of the mandibular arch bends ventralwards is very marked.

Fig. 12.—Ventral view of same head drawn to a smaller scale. The mouth has much widened, and the posterior slit-like part has almost entirely disappeared. The anterior part of the mandibular arch has a process towards the middle line. The hinder end of the body has been tilted upwards so as to bring the fronto-nasal process into view.