STUDIES ON THE EMBRYOLOGY OF THE SIPUNCULIDÆ.

I. THE EMBRYONAL ENVELOPE AND ITS HOMOLOGUE.

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XXII.

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(PLATE XXXII.)

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I. INTRODUCTION.

The peculiar embryonal envelope of Sipunculus nudus, with its associated amniotic cavities described by Hatschek ('83), has hitherto been regarded as a structure *sui generis.*

Hatschek ('80) discovered nothing of a similar nature in Echiurus; and yet among the annelids the Echiuridæ may perhaps be regarded as the nearest allies of the sipunculids. Nor did the observations of Selenka ('75) upon Phascolosoma throw any light upon this remarkable feature in the development of Sipunculus.

So little has been known of the embryology of this interesting group that at the suggestion of my friend Dr. C. A. Kofoid I undertook the study of the development of Phascolosoma gouldii Diesing. My work was begun in the summer of 1893 at the laboratory of Dr. Alexander Agassiz at Newport, R. I. Observations made at Newport proved this locality to be so favorable for my work that on the succeeding year by the kindness of Mr. Agassiz I continued my studies there, and was able to follow the development of the trochophore and larva until the latter had reached the age of thirty days. My first attempts to study the cleavage stages, while still a student under Dr. Mark at Harvard University, met with only a partial success, owing to the difficulty presented by the thick and highly refractive yolk-membrane (zona radiata) to staining and preparing in balsam the somewhat opaque eggs and embryos of this species. After repeated attempts at Wood's Hole, Mass., during the summers of 1896 and 1897 to obtain material for this study, I went to the Laboratoire Lacaze-Duthiers at Roscoff in Finistère, where I enjoyed the hospitality of the founder. There in the summers of 1898 and 1899 I was able to work out somewhat in detail the cleavage of the beautifully transparent egg of Phascolosoma vulgare Blainville, to compare the arvæ of this species with those of P. gouldii, and to collect material for further investigation. The work was extended by studies in P. gouldii at Wood's Hole during the summers of 1900 and 1902.

I have made several attempts to fertilize the eggs of Sipunculus, once on October 1 at the laboratory of the Collège de France at Concarneau in lower Brittany, once in July at Roscoff with specimens collected at Trez Hir near Brest, and several times during the winter months at Naples. There is reason to believe that renewed efforts at Concarneau and Trez Hir, where Sipunculus is abundant, or possibly at Naples, would meet with success. The studies should be carried on, whether in Brittany or at Naples, during the spring or early summer. I have been unable to verify the observations of Hatschek ('83) upon Sipunculus except as regards a single stage in the larval development of S. tessellatus Kef. taken in the tow at Naples.

I wish here to make hearty acknowledgment to all who have aided me in various ways in carrying on these studies, especially to Mr. Alexander Agassiz and likewise to Dr. Mark, whose interest in the work and helpful advice have been of great value to me. I am indebted also to the members of the respective staffs of the Zoological stations at Roscoff and at Naples, to Professor Fabre-Domergue, and not least to Professor Korschelt, who generously extended to me, while in Europe, the privileges of his laboratory at Marburg.

The present paper deals especially with those facts in the development of Phascolosoma which throw light upon the nature of the embryonal envelope in Sipunculus, and hence is limited in scope to a consideration of the ectoderm of the trochophore. A more complete account of the embryology of Phascolosoma will soon be published.

II. THE EMBRYONAL ENVELOPE IN SIPUNCULUS.

To make clear the nature of the embryonal envelope of Sipunculus, it will be well to remind the reader of the main features of the development of that form as described by Hatschek ('83). After a cleavage in which the blastomeres are of nearly equal size, the slightly larger cells at the vegetative pole become invaginated, and the embryo assumes the shape of a gastrula which has the more essential features of a trochophore (Pl. XXXII, Fig. 1). There is an apical plate which bears long cilia, and a circular band, composed of two or three rows of ciliated cells, corresponding in position to a prototroch. At the posterior pole is the invagination of endoderm, and a pair of mesoderm pole-cells project from the dorsal lip of the blastopore into the well-marked segmentation-cavity.

At this stage not only do the cells at the vegetative pole become separated from the zona radiata, but at the active pole the marginal cells of the apical area, which surround the four characteristic rosette cells, become separated from the zona radiata and sink, forming a deep ring-shaped furrow—the amniotic cavity of the head (Pl. XXXII, Figs. 1–5, *cav. am. ce.*).

Thereupon the closure of the blastopore ensues by a growth ventrad and forward of the ectoderm of its dorsal lip, at which point the mesoderm cells are situated (Figs. 2, 3, 4). This process results in the formation of a median somatic plate (Rumpfplatte), which is to furnish the whole of the definitive ectoderm of the trochophore except the apical plate.

Simultaneously with this process occurs the formation of the embryonal envelope or serosa. The cells of the body between the apical and somatic plates go to form this membrane. These cells, which are arranged in two or three rows as seen in optical section, are not only shown by their position and number to be prototroch cells, but their probable nutritive function and final dissolution are phenomena that are strangely similar to the function and fate of the prototroch cells of Phascolosoma, as will be shown in the next section. In brief these cells in Sipunculus become flattened out against the egg-membrane, spreading backward past the somatic plate till they reach the posterior pole and completely enclose the embryo (Figs. 2, 3, 4).

In the process of closure the cells become thinner and thinner, in marked disproportion to that decrease in thickness which is due to their spreading out. The process of wasting away continues even in later stages, so that Hatschek is inclined to the opinion that the serosa is giving off material which serves to nourish the embryo, a belief which my studies on Phascolosoma tend to corroborate. Meanwhile the boundaries of the cells in the serosa and even the nuclei disappear. The cells thus degenerate, and their substance seems to be in part absorbed.

Even before the closure of the serosa at the vegetative pole the ring-shaped furrow which surrounds the four characteristic cells at the centre of the apical plate (Kopfamnionhöhle) is continued backward in the median line by a mid-dorsal furrow (Amnioncanal), which is formed by the sinking of a double row of cells and their consequent separation from the zona radiata (Figs. 7, 8). This furrow passes backward into a wide cavity beneath the somatic plate at the posterior or vegetative pole of the embryo (Rumpfamnionhöhle). In other words, all of the ectoderm cells except those which bear cilia have become detached from the zona radiata and sunken beneath the surface; these areas, as I shall show presently, are exactly represented in Phascolosoma by characteristic small cells, which, however, do not sink from the surface.

The somatic plate of Sipunculus, over which lies the amniotic cavity of the trunk (Figs. 2–6, 8), extends forward in the mid-ventral line of the embryo to the blastopore, and, after the closure of the latter, to the apical plate (Figs. 4, 5). It consists along this ventral side of a narrow tongue-shaped band (Fig. 6, *tab. so. v.*). At the posterior end of the embryo, and especially on the dorsal side, it is, however, expanded into a broad sheet (*tab. so. d.*), from which the double row of sunken cells extends forward along the mid-dorsal line through a break in the serosa to the apical plate (Fig. 8).

It is necessary here to summarize only in part Hatschek's observations, and it will be sufficient to point out in conclusion that, by the growth of the somatic plate chiefly from the dorsal side forward and laterally, the definitive surface of the young larva is completed. The mid-dorsal double row of cells first disappears, possibly to form a part of the serosa. The broad dorsal part of the somatic plate then begins to extend forward and laterally, becoming thinner than the ventral, the lateral line of union of the two being situated far toward the ventral side. It should be noted in passing that in its growth the somatic layer of mesoderm outstrips the ectodermal somatic plate, so that for a time even after the cœlom is established, the serosa forms the ectodermal covering of the body proper, beneath which lie the two layers of mesoderm enclosing the cœlom and beneath them the endoderm (Fig. 6), a stage corresponding exactly to the trochophore of Phascolosoma before shedding the egg-membrane.

III. THE PROTOTROCH OF PHASCOLOSMA.

In a form so closely related to Sipunculus as Phascolosoma we should expect to find a similarity in the main features of development, and it has seemed very remarkable to me that a structure of such prominence as the embryonal envelope or serosa of Sipunculus should not have its homologue in Phascolosoma.

I shall endeavor to make it clear that in Phascolosoma not only the serosa is represented, but that the rest of the ectoderm is disposed in an essentially similar manner to that in the Sipunculus embryo, the most obvious differences being those due to the presence in the egg of Phascolosoma of a much larger amount of yolk than in that of Sipunculus. The two species of Phascolosoma to which I have given most attention, namely, P. gouldii Diesing of the American coast and P. vulgare Blainv. of the British Channel, differ from each other in their development in slight details; the egg and trochophore of the former are more opaque than in the European form, owing to a difference in the amount of yolk.

The cleavage in Phascolosoma is very unequal. The egg like that of certain of the nemerteans (Micrura cæca, Cerebratulus leidyi, and C. lacteus) is remarkable for the large size of the first set of micromeres and their descendants; these "micromeres" in the eight-cell stage slightly exceed in size the macromeres, except in quadrant D. Thus a preponderance of yolk is located in the "active" half of the egg; and the prototroch cells of the trochophore, which arise from this half, are laden with large yolk-granules coarser and more abundant than those of the endoderm.

In the 48-cell stage of P. vulgare at the age of about ten hours, cilia begin to make their appearance upon the sixteen large "primary" prototroch cells,* and a little later a tuft of long flagella appears upon the apical plate. The latter consists at this stage (Fig. 9) of a comparatively large rosette in the angles of which are four cross-cells, while radiating outward from its four points are two intermediate cells in each quadrant. Thus the active half of the egg in the 48-cell stage consists not of 24 cells but of 32, leaving only 16 cells at the vegetative pole.

The changes which ensue at the anterior pole in the establishment of a complete trochophore involve the division of the cross and intermediate cells into a large number of very small cells. The rosette cells, however, divide probably only once, leaving a definitive diamond-shaped rosette composed of four comparatively large cells which give rise to long sensory flagella (Fig. 11, *ros.*). This definitive rosette becomes surrounded during the next ten hours by the small cells of the apical plate, like an island in the midst of a circular pool (Fig. 11). A dorsal cord (Fig. 12, *cd. d.*) composed of similar small cells extends backward in P. vulgare from the apical plate through a mid-dorsal break in the prototroch to the somatic plate behind the prototroch. Thus the ectodermal areas in the embryo of Phascolosoma correspond in all respects to those in Sipunculus (Figs. 7, 8), except that in Phascolosoma the cells which surround the definitive rosette, those of the mid-dorsal cord, and those of the somatic plate of ectoderm do not sink away from the zona radiata to form amniotic cavities as the corresponding cells do in Sipunculus.† That the latter should sink away from the surface in Sipunculus is not extraordinary, since even in the early cleavage stages the blastomeres are separated from the egg-membrane (zona radiata) by an obvious space. The blastomeres of the vegetative pole in Sipunculus apparently never touch the adjacent zona radiata. The yolk-laden egg of Phascolosoma on the other hand completely fills the zona radiata; and all of the blastomeres, whether ciliated or not, are at all times closely applied to the inner surface of the yolk-membrane (compare Figs. 1 and 10).

Having observed that the cells of the apical plate, those of the mid-dorsal cord, and those of the somatic plate correspond closely in the two forms, the only other ectoderm cells that remain to be considered are those of the prototroch of Phascolosoma and of the serosa of Sipunculus. It is impossible to compare these two structures cell by cell until we have some knowledge of the cell lineage of Sipunculus, but there cannot be the slightest doubt that the serosa in Sipunculus represents in

* A fuller account of the lineage of the prototroch cells in Phascolosoma, including the three "secondary" cells, will be presented in a later paper.

† It is hardly necessary to call the reader's attention to the striking resemblance between the sipunculid and the annelid trochophore, as regards the arrangement of the ectoderm.

general the prototroch of Phascolosoma. The arrangement of the cells of these structures in two or at most three rows in an equatorial band, separated in front, dorsally, and behind by tracts which correspond essentially in the two forms, as well as their large size and uniformly ciliated condition in each form, make the general homology certain.

Before describing the fate of the prototroch in Phascolosoma, it will be well to point out the fact that in P. vulgare a zone of prominent cells bearing a postoral circlet of long cilia is formed behind the prototroch and separated from it by a narrow interval (Figs. 13, 14). This postoral circlet is quite independent of the prototroch proper, and is retained long after the latter has ceased to exist. Thus it develops earlier than the postoral circlet in Sipunculus, which appears in a similar position only after the prototroch cells have slipped back over the somatic plate and formed the embryonal envelope. In Sipunculus the postoral circlet is formed within the amniotic cavity, and appears from Hatschek's observations to become functional as a locomotor organ only after the casting off of the serosa; in Phascolosoma, on the other hand, the cilia, like those of the aboral band covering the prototroch proper, penetrate the zona radiata and serve even before the shedding of that membrane as the organs of locomotion for the trochophore. During the shedding of the zona radiata they either slip through its pores like the flagella of the apical plate in both Sipunculus and Phascolosoma, or the membrane itself splits open along the line of their connection with the body. The postoral circlet in Phascolosoma gouldii is vestigial and in most individuals entirely absent; but a preoral circlet in front of the adoral band of the prototroch (Fig. 15) serves in this species for a short time as the chief organ of locomotion.

Our entire knowledge of the development of Phascolosoma, with the exception of a few scattering notes, has been based upon a single brief paper by Selenka ('75) in which he describes in an excellent manner for that time, but in a primitive and incomplete way, a few of the cleavage stages, the trochophore and two stages in the development of the young larva. In this paper he asserts that the zona radiata (Dotterhaut) is never shed, but becomes transformed gradually into the cuticula of the larva. Similar statements that have been made in regard to various annelids seem to me to be open to the suspicion that there has been a failure to observe that critical stage in which the zona radiata and cuticula are both present. My experience with Phascolosoma has shown how readily this stage may be overlooked, and I quite agree with Eisig ('98, p. 98) that "sobald nur das Augenmerk speciell hierauf gerichtet wird, auch noch weitere Fälle von Häutungen des Embryos zur Beobachtung gelangen und dementsprechend die Angaben über die Verwandlung der Eihaut in die Cuticula der Larve oder des Wurmes allmählich aus der Litteratur verschwinden werden."

I have conclusive evidence that both the trochophore of P. gouldii and that of P. vulgare at the time of their transformations into the young larvæ (forty-eight to fifty-eight hours approximately) shed the zona radiata, for not only have I watched the whole process and made preparations which show clearly the ruptured membrane still clinging to the head, but sections of trochophores from forty to forty-five hours old uniformly show beneath the old yolk-membrane, which still retains its characteristic pore-canals, a well-marked cuticula (Fig. 15). The latter is not as highly refractive as the zona radiata, and at its first appearance is slightly granular. During the process of shedding the zona radiata, the strong cilia of the postoral band in P. vulgare and the similar cilia of the preoral band in P. gouldii slip through the pores of the membrane. Some of the flagella of the apical plate do likewise, but only remnants of the prominent apical cilia of the trochophore remain upon the larva.

IV. DISSOLUTION OF THE PROTOTROCH IN PHASCOLOSOMA AND COMPLETION OF THE DEFINITIVE BODY-WALL OF THE LARVA.

At the age of about forty-four to fifty hours the trochophore is still enclosed within the thick zona radiata and covered by a thin cuticula. The thickness of this cuticula is greatest at the posterior end of the body, where it is about half that of the zona radiata. It entirely covers the anterior end of the body, including the prototroch cells, which are soon to disappear.

The retractor muscles have already made their appearance at this time, with their origin in the ectoderm of each side of the posterior end of the trochophore and their insertion in each side of the apical plate (Figs. 15, 16). These muscles soon begin to operate, repeatedly drawing the head backward against the endoderm of the newly formed archenteron. This process results in a pressure upon the surrounding prototroch cells, which are of extraordinary size and completely enclosed by the thin cuticula (Fig. 15).

The somatic plate of ectoderm at this time forms a continuous layer over the subumbrellar region of the trochophore, which we may henceforth call the trunk. It is extended forward on the dorsal side and is united in P. vulgare to the apical plate by the dorsal cord of ectoderm, which has been already described as composed at its narrowest part at first of only two rows of cells. On the ventral side it consists at this time of a band of cells which extends forward on each side of the stomodæum. Thus the prototroch cells occupy two large areas, one on each side of the anterior part of the body, and these are connected ventrally in front of the stomodæum (Figs. 12, 14).

These cells now degenerate; their yolk, and finally even their nuclei pass backward into the newly formed cœlom (Fig. 15). The somatic plate or ectoderm of the trunk meanwhile is growing forward and ventrad beneath the prototroch on each side as in Sipunculus, dorso-lateral proliferations of the apical plate extend backward, and thus the definitive body-wall of the larva is finally completed. The dissolution of the prototroch cells in P. gouldii is effected as follows: The inner side of the cells first shows signs of breaking down in that the cell-wall is dissolved, and the yolk-granules pass inward and backward into the cœlom (Fig. 15). The outer parts of the cells, however, remain intact for a considerable time and still contain nuclei. When their dissolution is complete and their contents in the form of yolk-granules have found their way backward into the body-cavity, the ectoderm of the trunk closes over the gap left by the passage backward of the substance of the prototroch cells, and becomes united to the apical plate laterally, as was previously the case upon the dorsal and ventral sides (Fig. 16).

I am of opinion that the mechanical pressure of the apical plate upon the disintegrating prototroch cells during the periods of contraction of the retractor muscles has an important part to play in crowding the remnants of the cells back into the cœlom.

The shedding of the zona radiata occurs simultaneously with the end of the process of dissolution of the prototroch and of the engulfing of its substance into the cœlom. The remnants of the zona radiata may be found still clinging to the heads of embryos in which the remains of the prototroch cells have sunken away from the surface. This appears to be a period fraught with considerable danger of rupture of the lateral walls of the head region, and individuals are not infrequently seen in which the substance of the prototroch has oozed out upon the surface of the body through the premature tearing of the zona radiata, the cuticula in that region being exceedingly thin. Hence it happens that the young larva, no longer a trochophore, remains for a longer time than usual in a condition of contraction as regards the retractor muscles until the prototroch region has healed over, so to speak, by the growth of the ectoderm of the sides of the trunk forward to the apical plate and over the region of the dissolving prototroch.

V. FATE OF THE PROTOTROCH IN THE SIPUNCULIDS.

From the foregoing account it is evident that there is an essential similarity between the prototroch of Phascolosoma and the serosa of Sipunculus. This similarity holds not only in the position and probable number of the cells and the arrangement of these between correspondingly apical and somatic regions of ectoderm, but also in the transitory nature of each structure and their common function. The cells which I regard as the prototroch in Sipunculus spread backward past the margin of the somatic plate, and form a complete embryonal envelope or serosa in which nuclei can no longer be seen; the serosa dwindles into an exceedingly thin layer, and its substance, according to Hatschek, is probably absorbed by the embryo. The remnant is finally cast off with the zona radiata.

Its homologue in Phascolosoma, on the other hand, appears as a typical prototroch of relatively huge size, which likewise becomes flattened out against the zona radiata, and covers a broad equatorial region of the trochophore; but it never forms an embryonal envelope, and at the time of the shedding of the zona radiata it is not cast off with this structure, but disintegrates and passes into the body-cavity.

Thus in Sipunculus probably, and in Phascolosoma surely, it is a nutritive organ. In Phascolosoma the cytoplasm of each prototroch cell becomes converted, before its final disintegration, into yolk-granules which, passing into the cœlom, completely fill the cœlomic fluid (Fig. 16) and form the chief source of nourishment for the larva during the first week. At the end of this period most of the yolk has been absorbed.

VI. PHYLOGENETIC SIGNIFICANCE OF THE PROTOTROCH.

Since no embryonal envelope was apparent in Phascolosoma, according to Selenka's brief account of the development, Hatschek raised the question as to whether the serosa of Sipunculus had been acquired during a comparatively short phylogenetic period from conditions like those in Phascolosoma without a serosa or whether, on the other hand, there had been an atrophy and loss of the structure in the latter form. We are now in a position to answer this question with some degree of certainty, or at least to form some definite opinions in regard to the matter, which is all that embryological evidence alone can enable us to do with questions of phylogeny.

The prototroch of Phascolosoma resembles in many respects that of annelids. The large primary prototroch cells of the former correspond precisely in origin to those of the annelids. There is evidence also that the prototroch cells of annelids undergo a degeneration similar in some respects at least to that in Phascolosoma. Thus Mead ('97, p. 261) states that in Amphitrite "The prototroch and paratroch before their actual disappearance undergo a marked degeneration. The cells shrink and become filled with yellow granules." The process of dissolution of the prototroch and the replacement of it by definitive ectoderm has not been described in Amphitrite, but aside from the question whether its substance is gradually absorbed *in situ*, as appears to be the case, or passes in the form of visible yolk-granules into the cœlom as in Phascolosoma, it is clear that there is in respect to the prototroch a remarkable similarity between the two forms.

Shedding of the prototroch, moreover, occurs both in the annelids and the mollusks. Eisig ('98, pp. 81, 108) describes the degeneration and casting off of the peripheral part of the prototroch in Capitella, and suggests that it may perhaps occur normally in Polygordius, in which Hatschek has observed that groups of ciliated prototroch cells, undergoing degeneration, are sloughed off. Hatschek, however, regards this as a pathological process and maintains ('78, p. 50) that the prototroch cells in Polygordius gradually diminish in height and assume the characters of other epithelial cells.

Meisenheimer (:01) sets forth the general homology between the velum of Dreissensia and the prototroch of annelids, which is evident if the former term be restricted to the two posterior rows of cells of the velum, so as to exclude the apical plate and "Dach des Velums" of Dreissensia. The vacuolization and flattening of the cells of the prototroch proper and the attenuation of those which form the roof of the velum, all of which are finally cast off, furnish some interesting points of similarity in the fate of the prototroch in a mollusk and in a sipunculid.

I have endeavored to show that the serosa of Sipunculus represents the remains of a degenerating prototroch equivalent to that of Phascolosoma, which in turn is homologous to the prototroch of mesotrochal annelids. Which of the three types represents the most primitive condition? Clearly it is the prototroch of the annelids. Waiving for the present the question as to whether the sipunculids have been derived from segmented or unsegmented ancestors, there can be little doubt that they sprang from forms in which the prototroch was, like that of the annelids, of moderate size and without the specially acquired functions of protection and nutrition which it performs in the sipunculids.

It is quite conceivable that the differences between the prototroch in Phascolosoma and in Sipunculus may have arisen as an effect of the presence or absence of yolk. The adaptation of form and habit to various quantities of yolk is evident even in the different species of Phascolosoma. Thus in P. gouldii there is a comparatively sluggish trochophore, the prototroch cells of which are heavily laden with yolk, so that this species rises little from the bottom. In this form the postoral circlet of cilia is only feebly developed. In P. vulgare there is less yolk, and the trochophore is more active; it remains at the surface for a longer time than the American form, and moves vigorously by means of a postoral circlet of cilia, even after the zona radiata has been cast off. There is, however, much yolk both in the prototroch and in the endoderm of this species, and consequently an epibolic gastrulation. In Sipunculus nudus, on the other hand, there is very little yolk, and the trochophore is markedly pelagic. It seems probable that the ancestors of Sipunculus possessed more yolk than at present exists in the embryo, and that during the acquisition of the pelagic habit the amount of yolk in the prototroch cells has been gradually reduced. The large superficial extent of the serosal or prototroch cells, the fact that their substance gradually wastes away, probably to be absorbed by the embryo, and the further consideration that in Phascolosoma the corresponding structure is an organ of nutrition lend favor to this assumption.

If this supposition is true, it is readily understood how it has come about that the non-ciliated cells of the body in Sipunculus lose their connection with the zona radiata and sink beneath it, thus giving rise to amniotic cavities. This supposition also offers an explanation of the invagination of the endoderm and the infolding of the somatic plate; nor is it difficult to imagine how the prototroch cells under these supposed conditions became spread out backward, slipping past the somatic and endoderm plates till they covered the inside of the entire zona radiata and formed the ciliated serosa. Accordingly the zone on which the postoral cilia were and still are developed in Sipunculus lies no longer behind the prototroch, as is the case in Phascolosoma, but beneath it; and the appearance of cilia upon this zone is deferred until the remnants of the surrounding prototroch or serosa are about to be cast off.

VII. SUMMARY.

A comparison of the development of Sipunculus, as described by Hatschek, with that of Phascolosoma leads to these results:

1. The following regions of the ectoderm of the trochophore are homologous in the trochophore stages of Sipunculus and of Phascolosoma:

(A) the apical region, with a characteristic definitive rosette at its centre;

(B) the mid-dorsal cord, which extends backward from the apical region through a break in the prototroch to the somatic plate;

(C) the somatic plate, which, owing to the yolk within the endoderm, in Phascolosoma never sinks away from the zona radiata as in Sipunculus;

(D) the prototroch, which in Sipunculus spreads out forward over the edge of the apical plate and backward over the somatic plate and forms the serosa. In Phascolosoma the sixteen huge primary prototroch cells are derived from the anterior half of the egg (first group of "micromeres," which, however, in the 8-cell stage exceed in size the "macromeres" except in quadrant D). They become flattened out against the zona radiata as in Sipunculus, though to a less extent. They are covered with the short adoral cilia, and contain the greater part of the yolk of the entire trochophore.

2. The prototroch cells in Phascolosoma undergo rapid dissolution from within outward, at the time when elongation of the trunk begins and shedding of the zona radiata occurs. Their substance, which has been largely converted into yolk, is now passed into the fluid of the newly formed cœlom, whence it is gradually absorbed during the growth of the larva. The serosa of Sipunculus according to Hatschek also appears to be in some measure a nutrient organ, though its remnant is cast off with the zona radiata, and not passed into the cœlom.

In Phascolosoma, as in Sipunculus, the dorsal ectoderm of the somatic plate grows forward and ventrad on each side of the body, closing over the region vacated by the prototroch (=the serosa) and joining two dorso-lateral proliferations of the apical plate which take part with it in the closure.

3. The prototroch of Phascolosoma and the serosa of Sipunculus have probably arisen from what may be called a typical prototroch, such as occurs in mesotrochal annelids, from which type the prototroch in Phascolosoma departs less than does that in Sipunculus.

The differences in the structure and fate of the prototroch in the two forms appear to be the immediate result of the presence or absence of yolk. Reasons are presented for believing that the ancestors of Sipunculus were provided with a yolk-laden prototroch, like that which occurs to-day in Phascolosoma.

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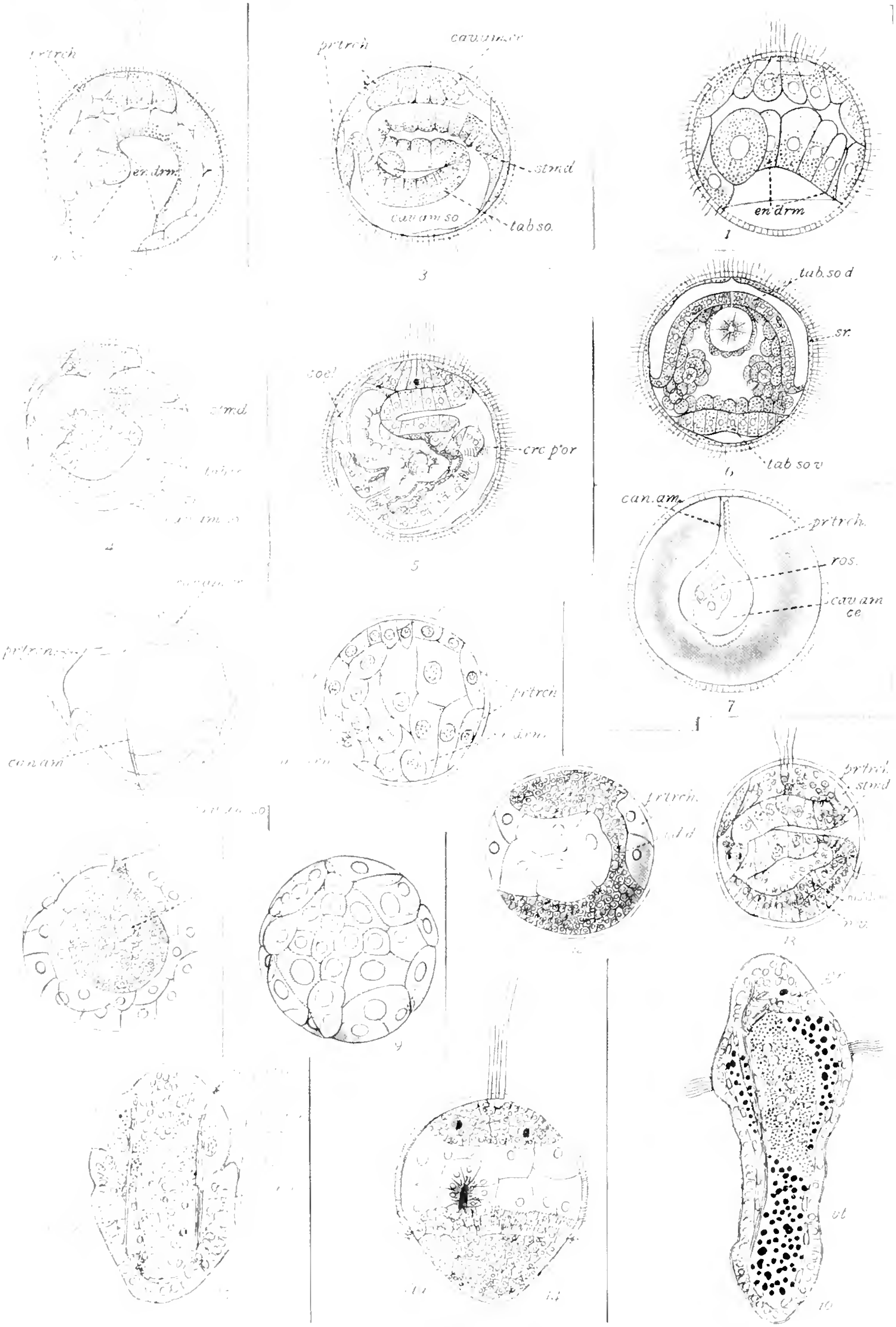
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pr.trch.
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7
pr.trch
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16

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EXPLANATION OF PLATE XXXII.

ABBREVIATIONS.

bl'po.	Blastopore.	*mu. rtr. v.*	Ventral retractor muscle.
can. am.	Amniotic canal.	*n. v.*	Ventral nerve-cord.
cav. am. cc.	Amniotic cavity of the head.	*pr'trch.*	Prototroch cells.
cav. am. so.	Amniotic cavity of the trunk.	*ros.*	Rosette.
cd. d.	Dorsal cord of ectoderm.	*sr.*	Serosa.
coel.	Cœlom.	*stmd.*	Stomodæum.
crc. p'or.	Postoral circlet.	*tab. apx.*	Apical plate.
crc. pr'or.	Preoral circlet.	*tab. so.*	Somatic plate of ectoderm.
cta.	Cuticula.	*tab. so. d.*	Dorsal somatic plate of ectoderm.
en'drm.	Endoderm.	*tab. so. v.*	Ventral somatic plate of ectoderm.
gn.	Supraœsophageal ganglion.	*vt.*	Yolk-granules.
ms'drm.	Mesoderm.	*z. r.*	Zona radiata.
mu. rtr. d.	Dorsal retractor muscle.		

PLATE XXXII.

Figures 1 to 8 of Sipunculus nudus were copied from Hatschek ('83). Figures 10 and 15 are of Phascolosoma gouldii. Figures 9, 11 to 14, and 16 are of P. vulgare. Figures 9 to 16 were drawn with the aid of an Abbé camera at a magnification of 250 diameters; Hatschek's figures were copied for a magnification of 210.

Fig. 1. Optical sagittal section of an embryo of Sipunculus nudus, showing the beginning of the invagination of the endoderm plate. The cells which surround the rosette at the animal pole show a tendency to sink, forming the amniotic cavity of the head (Hatschek, '83, Taf. I, Fig. 8).

Fig. 2. Optical sagittal section of an older embryo, showing the establishment of the somatic plate of ectoderm; the cells of the serosa have slipped over and past the edge of the somatic plate (Hatschek, '83, Taf. II, Fig. 17).

Fig. 3. Optical sagittal section, immediately before the closure of the blastopore (Hatschek, '83, Taf. II, Fig. 23).

Fig. 4. Optical sagittal section, after closure of the blastopore and formation of the stomodæum (Hatschek, '83, Taf. III, Fig. 25).

Fig. 5. Side view combined with optical section, showing the postoral circlet of cilia (Hatschek, '83, Taf. IV, Fig. 37).

Fig. 6. Optical cross-section through a similar embryo, taken immediately behind the postoral circlet (Hatschek, '83, Taf. IV, Fig. 38).

Fig. 7. Sipunculus embryo seen from the active pole (Hatschek, '83, Taf. II, Fig. 14). The rosette, surrounded by the amniotic cavity of the head, and the mid-dorsal amniotic canal are shown; the further course of this canal toward the vegetative pole and the transition of its margin into the free rim of the serosa are shown in broken lines; the position of the serosa (=prototroch) is defined. This figure should be compared with Figure 11.

Fig. 8. An older embryo of Sipunculus than that shown in Figure 7. It is seen from the dorsal side, and shows the amniotic cavities of the head and of the trunk, and the connecting mid-dorsal canal (Hatschek '83, Taf. III, Fig. 31). The cells which underlie these spaces correspond respectively to the apical and the somatic plates and to the connecting mid-dorsal cord of ectoderm in Phascolosoma. The prototroch or serosa cells at this stage have slipped backward past the somatic plate and closed together at the posterior pole. This figure should be compared with Figure 12.

Fig. 9. Egg of Phascolosoma vulgare in the 48-cell stage, 6 hours and 40 minutes after fertilization. Drawing of an unstained egg in glycerine, showing the cells of the active pole. The rosette is stippled; the cross-cells are marked with parallel lines; the intermediate cells are shaded very lightly, and the primary prototroch cells upon the margin are shaded more deeply.

Fig. 10. Longitudinal sagittal section of egg of Phascolosoma gouldii, between 15 and 20 hours old, showing the rosette and intermediate cells of the apical plate and cells of the prototroch. Within are shown endoderm and mesoderm cells. Compare with Figure 1.

Fig. 11. Surface view of a young trochophore of P. vulgare, 25.5 hours after fertilization, showing the definitive rosette in the middle of the apical plate, which in turn is surrounded by the cells of the prototroch. The prototroch consists of nineteen cells. The mid-dorsal cord is shown at its junction with the apical plate Compare with Figure 7.

Fig. 12. Left-dorsal view of a trochophore of P. vulgare, 25.5 hours after fertilization, showing apical plate, mid-dorsal cord and somatic plate of ectoderm, besides the intervening prototroch. Compare with Figure 8.

Fig. 13. Section of a trochophore of P. vulgare 39 hours after fertilization. The plane of section is approximately sagittal. Compare with Figure 5.

Fig. 14. Ventral view of a trochophore of P. vulgare, about 45 hours old, to show the prototroch. The adoral cilia which cover it are represented only along the margin. The postoral circlet of cilia appears behind the prototroch, and is separated from it by a distinct interval. The apical region, with rosette, eye-spots, and sensory flagella, and the rapidly growing trunk are shown. A distinct cuticula is already to be seen in the trunk region beneath the zona radiata. Drawn from a living specimen, with details added from a preparation of a specimen of the same age. Compare with Figure 5.

Fig. 15. Parasagittal section of a young larva of P. gouldii, 57 hours old, just previous to the casting off of the zona radiata, under which a continuous cuticula has already been secreted. The dorsal and ventral retractors of the right side of the body are shown in a state of partial contraction. Yolk-granules are seen passing out of the prototroch into the clœom, where the entire substance of the prototroch is soon to be engulfed.

Fig. 16. Parasagittal section of a larva of P. vulgare, 51 hours old but more advanced in development than the larva represented in Figure 15. Yolk-granules of different sizes are seen in the cœlomic fluid, in which they flow freely back and forth at every contraction and elongation of the body, which attend the oft-repeated introversions of the head. The postoral circlet of cilia are still active; a single (left-ventral) retractor muscle, and other features are shown.