

## **Observations on the development of Agelena naevia / by William A. Locy.**

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### **Publication/Creation**

Cambridge : Printed for the Museum, 1886.

### **Persistent URL**

<https://wellcomecollection.org/works/gb56b7jt>

### **Provider**

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Bulletin of the Museum of Comparative Zoölogy,

AT HARVARD COLLEGE.

VOL. XII. No. 3.

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OBSERVATIONS ON THE DEVELOPMENT OF AGELENA NAEVIA.

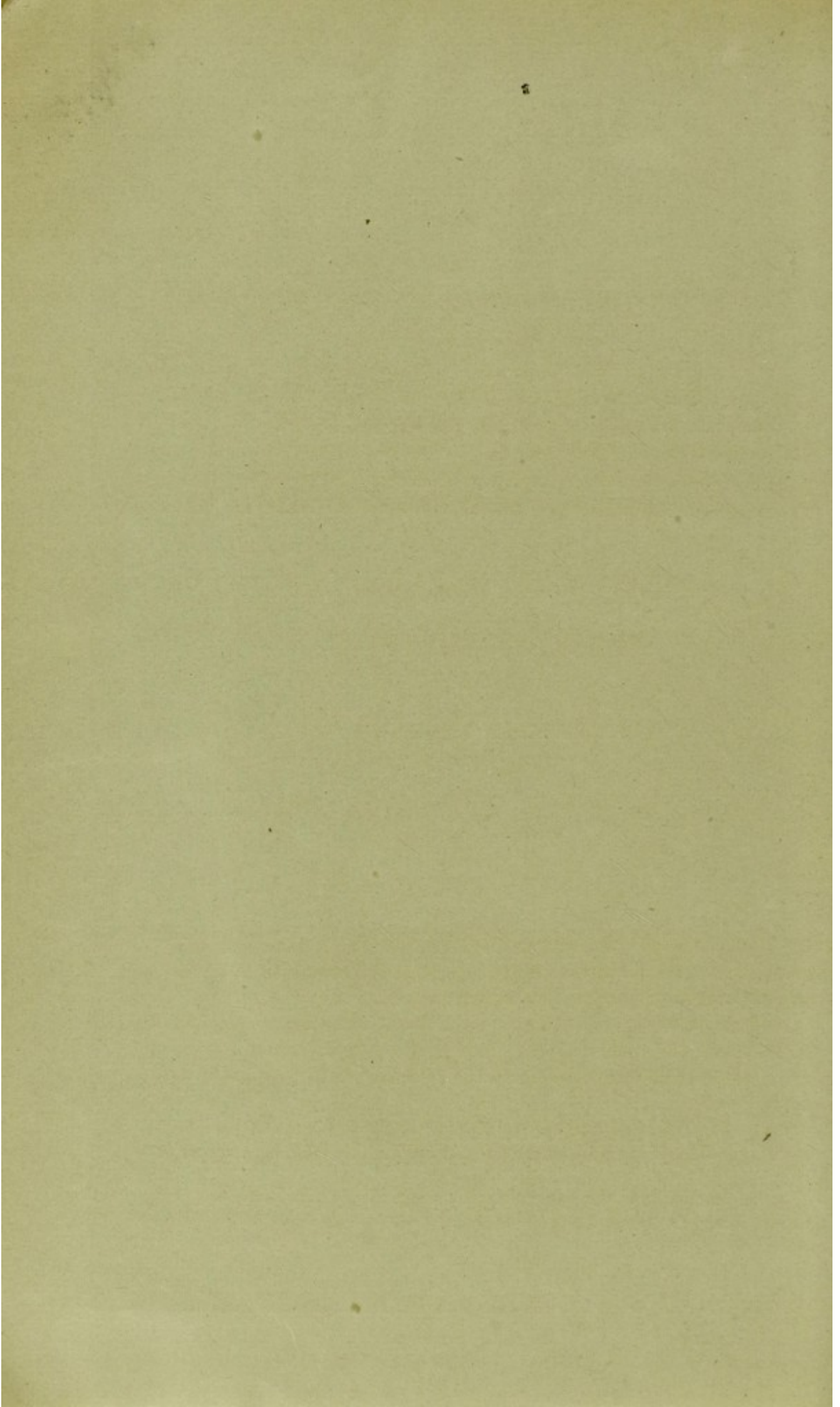
BY WILLIAM A. LOCY.

WITH TWELVE PLATES.



CAMBRIDGE:  
PRINTED FOR THE MUSEUM.

JANUARY, 1886.




Museum of Comparative Zoölogy, Cambridge, Mass.

*With the compliments of*

*ALEXANDER AGASSIZ.*





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No. 3. — *Observations on the Development of Agelena navia.* —

By WM. A. LOCY.\*

SEVERAL memoirs have been published on the development of the Araneina, but the results attained are still unsatisfactory on account of the disagreement of authorities, and the limited extent to which the method of sectioning has been employed in studying the subject. Up to the present time only a single memoir, illustrated by figures of actual sections, has appeared.

Valuable as were the works of the earlier writers, Herold ('24), Rathke ('42), and Von Wittich ('45 and '49), they now are principally of historical importance, since their labors were performed either before the announcement of the cell theory, or before it had gained general recognition, and before embryology had attained its pre-eminence among morphological studies.

Claparède ('62) made extended observations on the external features of development, but did not discuss the preblastodermic period nor the period of the revolution of the embryo.

Salensky ('71) published in Russian a memoir, the figures illustrating which show critical observations on the external features of development. He was the first to figure the "rudimentary terga" of the period of revolution, and also the development of the procephalic lobes.

In a short paper on the development of Pholeus, Emerton ('72) confines his observations to the external features of development. He figures the polygonal areas of the blastema, and erroneously concludes that they are blastodermic cells without distinct nuclei. The relation of the primitive cumulus to the ventral plate is well figured.

Balbiani ('73) has produced one of the most satisfactory memoirs yet written; he figures and describes in detail the external features of the early stages of development up to the period of the formation of the appendages.

Ludwig's ('76) observations were confined to the formation of the blastoderm, and are at variance with Balbiani's, mainly in denying the exist-

\* Contributions from the Embryological Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the direction of E. L. Mark. No. VIII.  
VOL. XII. — NO. 3.



ence of the peripheral layer of protoplasm that is divided into polygonal areas prior to the appearance of the blastoderm.

Barrois ('78) added to what was already known an extended description, with figures, of his so-called limuloid stage, and gave notes, without figures, on the development of the germinal layers.

Balfour ('80) was the first to produce figures of actual sections to illustrate the history of the germinal layers. Unfortunately, he had no material for the preblastodermic period.

Sabatier ('81) contributes notes on the formation of the blastoderm, and also on the yolk nucleus of spiders' eggs.

Schimkewitsch ('84) offers the latest contribution to the subject in a preliminary notice in the *Zoologischer Anzeiger* for August 18, 1884, which embraces notes on the entire development.

### I.—The Egg.

The eggs of *Agelena navia* are very abundant in the autumn. Those for the present study were obtained near Cambridge, Mass., from September 15 to October 15. They exist in cocoons of white silk attached to the underside of fence boards or loosened bark, and in other sheltered places. This species, as well as others, continues to deposit eggs in captivity, thus furnishing a ready means of obtaining freshly laid material.

*Treatment.* — For observations on fresh material the long-used method of immersing the eggs in oil is indispensable. The oil should be perfectly clear and scentless. In hardened eggs the external features can be studied to great advantage by mounting in alcohol after they have been shelled and stained; the structures previously obscured by the chorion thus become properly exposed. Before using this method I was unable to trace the "rudimentary terga." Another valuable method for surface study consists in clearing the already stained egg in clove oil. I have found this especially applicable in determining, by means of optical sections, the thickness of the blastoderm on entire eggs.

In the important work of preparing eggs for cutting, experiments were made with several reagents. The most satisfactory method of treatment proved to be the very simple one already long in use. The eggs were heated in water to about 80° C, and cooled slowly, after which they were passed successively from weak to stronger grades of alcohol.

Good results were also obtained with Perenyi's fluid, which renders the yolk less brittle, but at the same time changes somewhat its characteris-



tic appearance, and therefore can be used only in connection with other methods.

Corrosive sublimate, either cold or hot, renders the eggs too brittle.

On account of the thickness of the chorion neither chromic acid nor acid alcohol can be entirely extracted, and osmic acid will not penetrate.

Borax carmine (Grenacher's alcoholic) has proved to be, on the whole, the best staining fluid. It is difficult to make any stain penetrate the material of the later embryonic stages and those subsequent to hatching, on account of the development of the cuticula. This difficulty was at length overcome by prolonged immersion in the staining fluid. In some cases seventy-two hours were required to obtain an adequate stain. Owing to the weak grade of alcohol used in making the stain, the eggs, to prevent maceration, were left in the stain only twenty-four hours at a time. They were then re-hardened, and after an interval immersed again in the staining fluid.

The brittleness of the yolk of spiders' eggs constantly produces crumbling of the sections. I have found that the yolk of eggs treated with Perenyi's fluid may be cut satisfactorily; in other cases I have used successfully Mason's collodion method.\*

*Composition of the Egg.*—The composition of the freshly deposited egg has already been described with accuracy in most particulars by Balbiani and others. In certain points, however, there has been neither agreement in descriptions nor great accuracy.

To make clear the subsequent account I shall describe briefly the constituent parts of the egg. It is enveloped by two membranes in contact with each other. The outer, or so-called chorion, is tough and homogeneous, with its external surface covered by granules, which vary in size and abundance in eggs of different species. In *Agelena nævia* they are arranged in a single layer, and do not offer any serious impediment to observations; in some species (e. g. *Epeira diadema*), however, they are several layers deep as well as very large, and must be removed to allow accurate observations. On removing these granules the chorion presents a finely punctate appearance, which is perhaps due, as Balbiani has suggested, to the impressions left by the granules. This membrane, unlike the chorion of insects, is added to the egg while it is passing through the oviduct, and like the egg-shell of *Apus* would fall into the category of "secondary egg membranes," as defined by Ludwig ('74).

\* See E. L. Mark, "Notes on Section Cutting," in the *American Naturalist*, June, 1885, p. 628.



Within the "chorion" is the structureless vitelline membrane which closely invests the substance of the egg. It is thinner than the chorion, from which it is easily separable after maceration. This membrane invests mature eggs before they leave the ovarian follicle, and is doubtless a product of the vitellus itself.

In making sections portions of these membranes were often cut. The vitelline membrane stains faintly in Borax carmine; the chorion retains its layer of outer granules, which are not dissolved in alcohol. There is, however, no trace of the areal arrangement of these granules, such as has been figured by Ludwig ('76) for *Philodromus limbatus*.

The egg is composed of finely granular protoplasm, in which is accumulated a large amount of nutritive material in the form of albuminoid yolk corpuscles, and minute fat globules. The albuminoid material is so distributed as to give the protoplasm a characteristic arrangement. The latter consists of a central mass enveloping the nucleus, a peripheral layer, and a coarse network connecting the two.

The peripheral layer (*couche germinative* of Balbiani) is the most striking feature in the arrangement of the protoplasm. It is in immediate contact with the inner surface of the vitelline membrane, and is so crowded with fat globules that Balbiani concluded erroneously that it is composed exclusively of such globules.

The central mass of protoplasm forms around the nucleus an irregularly limited, spheroidal envelope, containing neither yolk corpuscles nor the fatty globules which are so characteristic of the peripheral layer. Its outer portion is continuous with branching protoplasmic strands, which form a coarse network around the yolk corpuscles.

According to the observations of Balbiani the "yolk nucleus" persists during a part, at least, of the embryonic development, and should therefore be mentioned as one of the constituents of the egg. There is also to be included the perivitelline fluid, which makes its appearance during the contraction of the vitellus. I have no positive information concerning the source of this fluid, but having found no evidence of its existence in a definite morphological condition before the contraction takes place, I rest upon the assumption that up to this time it is uniformly distributed through the formative portion of the vitellus.



## II. — The Embryo.

For convenience in describing the development of the embryo, the following periods may be recognized : —

- (1.) The preblastodermic period, in which are embraced the changes in the mature egg up to and including the formation of the blastoderm.
- (2.) The period from the completion of the blastoderm to the formation of the rudimentary appendages, embracing, (*a*) the invagination, (*b*) the stage of the primitive cumulus, (*c*) the formation of the ventral plate, and (*d*) the division into protozonites.
- (3.) The period from the appearance of the appendages to the reversion of the embryo.
- (4.) The period of reversion.
- (5.) The period from the reversion to the hatching of the embryo.

1. *Preblastodermic period.* — The superficial and internal changes, although going on simultaneously, may be more easily described if considered separately. The surface changes can be watched on the living egg, and have been already thoroughly studied; but it is impossible to understand fully these changes without that knowledge of the internal phenomena which is to be obtained only by the aid of sections. The lack of this method of study has led several previous observers into errors of interpretation.

My earliest observations on the eggs of *Agelena nævia* were made a few (probably not more than three or four) hours after their deposit. At this time the polarity of the egg is very apparent; one hemisphere is characterized by small yolk corpuscles packed closely together, though not joined in masses, and the other by agglomerations of larger yolk corpuscles. The irregular masses thus formed are separated by spaces in which are found smaller isolated corpuscles like those which distinguish the opposite hemisphere.

Balbiani ('73) was the first to give an adequate account of the surface changes which occur during this period, in which the peripheral layer of protoplasm is principally concerned. We shall see by following the history of this protoplasmic layer, that it is the equivalent of the *blastema* observed in the eggs of many insects (Diptera, Phryganids, etc.), and Crustacea (crab, etc.), and I shall so designate it hereafter.

Ludwig ('76) and Barrois ('78) have both called in question the accuracy of Balbiani's observations as to the peculiarities of the blastema. My own observations are more in agreement with those of Balbiani, which they serve in a measure to confirm.



In freshly laid eggs this layer is in contact with the vitelline membrane, but early becomes separated from it by the contraction of the vitellus. The perivitelline fluid which makes its appearance during this process is coagulable by heat and is also stainable. At first the contraction of the egg is uniform on all sides, but soon it takes place more rapidly on one side, thus giving rise to a flattened surface (compare Fig. 5), upon which the ventral plate is afterwards established. Through the pressure of this contraction the blastema is moulded upon the peripheral yolk corpuscles into regions that correspond in position and size with the underlying corpuscles. Owing to mutual pressure these regions become regular hexagonal areas, (Pl. V. figs. 24, 25,) and resemble the subsequently formed cells of the blastoderm. The absence of nuclei is the fundamental feature that at once distinguishes them from the blastodermic cells, though they have frequently been mistaken for such on the supposition that the nuclei were obscured.

The division of the blastema into areas as described above is a very early phenomenon. At the time of my first observations a number of faintly marked areas had already made their appearance at the more active (animal) pole. At this time they could not be detected upon the opposite hemisphere; but after a short interval they also made their appearance there in isolated patches; finally they covered the entire surface of the egg. At the outset the boundary lines of the areas are very faint, but they become more distinct as the contraction of the vitellus continues. In some places the yolk corpuscles become separated from the blastema by a more rapid contraction of the interior protoplasm, and then the polygonal areas in such regions remain only partially outlined and incomplete, as described and figured by Balbiani ('73, Fig. 2).

After the areas are definitely formed the yolk corpuscles sometimes shift their original positions, and thus cease to coincide with the areas, since the latter do not at the same time undergo corresponding changes.

The next alteration in the surface makes its appearance only after the lapse of a considerable interval (twelve to forty-eight hours); this led Balbiani to assert, erroneously, that the egg is undergoing a period of rest. Sections show on the contrary, that the interim is one of great internal activity, during which repeated divisions of the nuclear substance lead to the formation of numerous cells which migrate towards the periphery. The appearance of some of these at the surface marks the beginning of new surface changes. The cells thus emerging from the yolk constitute the primary blastoderm; they first appear in the interspaces between the yolk corpuscles, but often migrate afterwards to



positions directly over the yolk corpuscles. Each cell embraces a large, clear, oval nucleus, which is surrounded by an irregularly radiating mass of protoplasm.

The influence of these nuclei upon the protoplasm of the blastema soon makes itself evident; a period of rearrangement supervenes in which the boundaries of the polygonal areas described above are gradually effaced, and the protoplasm of the blastema, as well as that which accompanies the migrating nuclei, is grouped into new masses with the nuclei as centres. The cells formed in this manner are at first large, irregular, and very unequal in size (Fig. 26), but by repeated divisions they become smaller, polygonal, and of more nearly uniform dimensions (Fig. 27). They ultimately form a continuous layer—the blastoderm—in the production of which the whole of the protoplasm of the blastema has been employed.

I now turn to a consideration of the internal changes which accompany the external features already described.

The structural and other peculiarities of the blastema in the eggs of spiders have been subjects of considerable discussion, and therefore deserve especial attention.

Balbani ('73) was the first to carefully study this layer,\* and to describe its division into areas.

Ludwig ('76) denied its existence, and located the polygonal areas described by Balbani on the outside of the chorion, they being due, in his opinion, to a peculiar arrangement of the granules covering the outer surface of that membrane.

Barrois ('78) admitted the existence of the blastema as a partial layer, but denied its division into areas; the latter, according to his view, are due to intersecting lines of granules located between the chorion and the vitelline membrane.

Sabatier ('81) agrees substantially with Balbani.

Thus the four observers who have discussed this topic have given three irreconcilable explanations of the polygonal areas that Balbani referred to the peripheral layer of protoplasm.

Sections of eggs during this period afford decisive evidence on the points under consideration. In the eggs of *Agelena nœvia*, at least, there can be doubt neither as to the existence of this layer, nor as to its division into areas. Figure 28 is from a section of an egg containing the first segmentation-nucleus (*nl.*), in which the blastema (*bl.*) is seen

\* It had been mentioned by earlier writers, Rathke ('37), Claparède ('62), and Emerton ('72), but they confounded it with the blastoderm.



to be of considerable thickness, and to envelop closely the peripheral layer of yolk corpuscles. An enlarged view of the same, given in Figure 30, Pl. VI., shows the finely granular structure and the vesiculated condition of the hardened blastema. It also shows how the blastema fits over the yolk corpuscles, and dips down between them. It is to these depressed regions that the boundary lines of the polygonal areas are due. Figures 31-33 are enlarged views of separate yolk corpuscles with the accompanying blastema.

The protoplasm of the blastema has a very characteristic appearance. In addition to the common character of being very finely granular, the protoplasm is throughout finely vesicular or spongy. The latter characteristic is especially marked in eggs heated in water to coagulate the protoplasm, and arises, I think, in the following manner. The fat globules described as filling the protoplasm of the blastema in the fresh egg are dissolved in the alcohol used for hardening purposes, and consequently leave in the protoplasm spheroidal spaces of nearly uniform size, which constitute the interstices. A discussion of the cause of the division of the blastema into areas will be found under general considerations at the end of the paper.

I have been unable, for the want of material, to trace the final changes in the germinative vesicle. In the earliest condition of the deposited egg that I have been able to procure there is a *single central nucleus* (Figs. 28, 29 *nl.*), which is doubtless the descendant of the germinative vesicle. This is the first segmentation-nucleus; it is large, oval, very finely granular, and surrounded by a spheroidal mass of protoplasm. The latter is in immediate continuity with the network of protoplasm, which extends throughout the egg. The yolk corpuscles in the vicinity of the protoplasm, which envelopes the nucleus, are much broken and become successively smaller in approaching the nucleus, and at length appear to merge into the finely granular protoplasm.

In the succeeding stage the central nucleus divides into two of equal size, which occupy a sub-central position (Fig. 34, *nl, nl'*). These nuclei have essentially the same character as the one already described. Fig. 36, from a two-cell stage of another egg, shows one of the nuclei with a central vacuole (*vl.*). The yolk is rudely divided at the same time, and having been previously arranged in radiating branched columns (*Deutoplasmasäulen* of Ludwig), now forms two groups of such columns (Fig. 34). It is probable that each of the two nuclei is divided into two others, and that each resulting therefrom is similarly divided, but I have not seen the four-cell stage. The next stage sectioned is one with eight



nuclei, all of which are nearer the centre than the surface of the egg. In an egg still further advanced, containing at least thirty nuclei, none of the cells have as yet emerged at the surface.

These internal cells are, however, continually migrating towards the periphery, and, as might be expected from other evidences of the bipolar condition of the egg, make their appearance first in that region which I have already designated as the animal pole. The further history of these cells after they have emerged at the surface has already been described under the head of surface changes.

The preblastodermic period, then, so far as I have been able to study it, begins with the incomplete separation of the protoplasm into two masses: one forming a thin layer at the surface — the “blastema” — and the other concentrated around a nuclear structure inferred to be a derivative of the germinative vesicle. The division of this nucleus is accompanied by a corresponding division of the central mass of protoplasm; a repetition of this process of division results in the formation of a number of cells which, migrating to the surface, appropriate the contiguous portions of the blastema until the latter ceases to exist as a separate layer; there is no evidence that the nuclei of any of these cells arise in any other way than by the repeated divisions of this single, central, first segmentation-nucleus; finally, the peripheral cells continue to subdivide as well as to receive accessions from more tardily migrating elements until a continuous single layer of cells — the blastoderm — envelops the egg.

2. The *second period* includes the changes from the formation of the blastoderm to the appearance of rudimentary appendages.

In the eggs of *Agelena nœvia* the blastoderm was established on the third day of development, the temperature being about 23° C during the day, and 19° to 20° C at night. Within certain limits\* the temperature has a marked influence on the rapidity of the development, and one can hasten or retard the growth by elevating or lowering the temperature. For a day or two the blastodermic cells undergo rapid division, and are, as a consequence, much reduced in size. There is a condition of the blastoderm intermediate between those shown in Figs. 26 and 27, in which the cells are regularly polygonal, but much larger than in Fig. 27.

My observations on the next surface change are not entirely satisfactory, as I have seen it in only one instance. It appeared late on the third day of development, and consisted of a depression at one pole similar to the depression in the surface of a peach at its stem end. This is

\* The eggs are killed by a temperature higher than 30° C.



probably the same phenomenon that Salensky ('71) described as a process of invagination, but to what extent it is comparable to a true invagination I am not at present able to say. Although a direct connection between this depression and the primitive cumulus has not yet been traced, it is certain that in point of time the depression is the forerunner of the cumulus, and the circumstantial evidence of their similar positions on the egg indicates a connection between the two.

The external feature just spoken of as the primitive cumulus originates as a thickening of the blastoderm, at one end of the flattened surface of the egg, and usually terminates in the production of a low conical elevation. In surface aspect the cumulus is ovoid, with its more pointed end directed towards the centre of the flattened surface, and it often shows a tendency to elongate in that direction. This patch of cells being rather opaque, appears whitish by reflected light, and dark by transmitted light. In some specimens it is considerably elevated above the surface of the egg, but in other cases it is only slightly or not at all raised. Upon hardened eggs the surface of the cumulus is often depressed by a median longitudinal furrow from which two or three smaller irregular furrows radiate towards its margin (Pl. I. fig. 4).

A second thickening, which I shall call the caudal thickening (*cdn. ca.*), soon makes its appearance on the flattened surface of the egg, at a distance of about  $80^\circ$  from the cumulus (Fig. 2.) It increases rapidly in size, spreading out most in the direction of the cumulus, and ultimately becomes shield-shaped. In the region between these two structures the ventral plate is gradually formed by a blastodermic thickening, which is not at first continuous with the two terminal thickenings. Indications of the existence of a ventral-plate thickening, which appears lighter by reflected light, are to be seen in the surface view shown in Fig. 2, Pl. I.

Immediately following the stage just described, the whole ventral surface of the egg becomes divided by a series of transverse ridges and furrows into protozonites (Pl. II. fig. 6). I have not the material to determine all the steps in the process, for the time involved in passing from the stage of the primitive cumulus to the protozonite stage is a comparatively short one. The earliest condition in the latter stage which I have examined shows three zonites and the cephalic plate. At this time the latter is only faintly outlined. It is a broad thickening, rounded towards the dorsal region of the egg, and fading into the protozonites on the ventral surface. The caudal plate does not become visible until two or three more zonites are established. It is similar in outline to the



cephalic plate. The addition of new zonites to those already existing goes on rapidly; the two anterior ones (those of the chelicerae and the pedipalpi) are cut off from the posterior end of the cephalic plate. They are late in making their appearance, and, as Balfour puts it, "lag behind" the others in their development. The other zonites are developed from the caudal plate.

Soon after the protozonites are first established they form ridges which reach nearly around the egg, and thus appear to radiate from the dorsal region. (Compare Emerton, '72, Figs. 8, 9.) They soon undergo concentration which so shortens the thickened ridges, that together they form a band about  $45^\circ$  wide on the ventral surface of the egg—the embryonic band. Fig. 6, Pl. II., gives a side view of an egg in which this concentration is well advanced but not yet completed. At the same time the embryonic band increases in length, thus extending in an antero-posterior direction further and further around the egg. When at length seven or eight protozonites are fully established, the band embraces approximately two-thirds of its circumference. At about this time also the rudimentary appendages begin to appear; these mark the commencement of the third period of growth.

The internal condition of the egg during the second period can be satisfactorily studied only by means of sections. I have made sections passing through the primitive cumulus in two directions, sagittal and transverse. In sagittal sections two features are conspicuous: (1) The ventral surface of the egg is clearly differentiated from the dorsal surface by the condition of the cells along its entire length (Pl. VII. fig. 41). (2) The cells in the region of the cumulus are arranged in several irregular layers. A thickening of the blastoderm has also arisen at the caudal eminence, and there is a tendency to thicken along the ventral region embraced between these two structures.

Figure 41 is from a sagittal section of the egg represented in Pl. I, Fig. 3; the cells of the ventral side are large and rounded or oval, while those of the dorsal side are much flattened. The cells of the primitive cumulus (*cum. pr.*) are conspicuous for their size; they are loosely arranged in layers. In some cases (Pl. VI. fig. 39) they are four layers deep.

Sections of eggs a little more advanced show a large number of cells along the ventral-plate region, and also at the caudal thickening.

Balfour's figure (l. c., Fig. 11) of this stage cannot be compared critically with my own, as he was uncertain about the direction in which the egg was cut; but from its close resemblance to my sections, I think it



safe to infer that he was wrong in supposing the larger accumulation of cells shown in his figure to represent the caudal thickening rather than the primitive cumulus. Fig. 39 is a *transverse* section through the primitive cumulus in the region of its greater width.

In radial sections of the egg during this stage the cells of the unmodified blastoderm appear lens-shaped, the deep surface being more convex than the outer, and contain each a single large nucleus, that is usually central in position (Fig. 40). They are frequently preserved in the process of division, their nuclei exhibiting the customary dumb-bell shaped figure (Figs. 42, 44).

The "interzonal filaments" are quite persistent, remaining distinguishable even after the formation of the dividing cell wall (Fig. 44).

The nuclei in nearly all the sections which were stained in borax carmine are in a condition very favorable for study. The filaments of chromatine are deeply stained, the nucleoplasm only faintly. The arrangement of the chromatic substance in the nuclei varies from a condition in which it is concentrated into a ball at the centre of the nucleus (Fig. 43), to one in which it forms a hollow shell near the surface of the latter.

Sections during the protozonite stage show that the blastoderm of the embryonic region consists of two distinct cell layers — the ectoderm and the mesoderm (Figs. 49, 45). The cells of the outer layer (ectoderm) are columnar (Fig. 45), and their nuclei, which are smaller than in previous stages, are very close together and much nearer the superficial than the deep ends of the cells. The cells of the inner layer (mesoderm) are not columnar but rounded cuboidal, and in general are much less regularly arranged than the ectodermic cells; their nuclei, which occupy the centres of the cells, do not at this stage present any other characteristic differences from the nuclei of the ectoderm. At a later period the nuclear elements of the mesoderm become spindle-shaped, and thereby can be readily distinguished from those of the ectoderm. As in the preceding stage, the cells of the non-embryonic or dorsal region of the blastoderm are much flattened, even more than previously, and only a single layer deep.

The cellular elements of the mesoderm are not everywhere definitely arranged, and the deep margin of the layer especially is irregular in outline; it partly envelops the yolk corpuscles, which are reduced to small fragments on the surfaces adjacent to the protoplasm, but it does not at this time form an uninterrupted layer.

The yolk corpuscles of this and succeeding stages are not absolutely



alike in constitution; some of them are stained deeply and appear homogeneous, while others are stained lighter and appear granular. During the whole of this period there continue to remain in the yolk mass a large number of cells, which are distributed through its substance at tolerably regular intervals. There is often a comparatively small amount of protoplasm enveloping the large angular nuclei of these yolk-cells, and about them the yolk corpuscles are more or less definitely grouped.

3. At the beginning of *the third period* the embryo still has a transversely banded appearance as in the protozonite stage; the concentration from the sides is completed, and about six zonites are distinguishable between the head- and tail-lobes. The zonites now begin to grow thinner in the ventral median line, and at the same time their ends become gradually more prominent and rounded. The small knob-like prominences at the ends of the zonites are the rudiments of the appendages, and in about two days after their first appearance (at the temperature stated) the six cephalo-thoracic appendages are fully established as represented in Pl. II. fig. 7. The two anterior pairs of appendages are much smaller than the four succeeding pairs, the latter being about equal in size. The appendages thus established correspond to the chelicerae, the pedipalpi, and the four pairs of ambulatory appendages of the adult.

Simultaneous with the growth of the appendages new zonites, derived from the tail-lobe, make their first appearance; the four anterior of these are very prominent, and a little later they bear four pairs of provisional appendages (Pl. IV. fig. 20, *pr. app.*). In this first part of the third period the head plate is faintly bilobed; the tail-lobe is broad and rounded.

A ventral view (Pl. IV. fig. 19) of the same egg (Pl. II. fig. 7) shows a faint median furrow, which marks the thinning out of the ectoderm in the median plane after the separation of the lateral halves of the underlying mesoderm. There are slight elevations just inside the bases of the limbs, best seen in optical section along the upper margin of the figure; they are the beginnings of the nervous ganglia.

At first the appendages grow out perpendicular to the axis of the body (Pl. II. fig. 7), but as they increase in length they curve towards the median line, as shown in Fig. 8. They are now indistinctly four-jointed. The central lumen, which can be observed readily in optical sections of the leg, is shown by actual sections to be a prolongation of the cavity of the corresponding mesodermic somite.

At the present stage — the last part of the third period — the head plate has become distinctly bilobed, a prominent upper lip composed of



two lateral elements has been developed, and the stomodæum has become faintly marked (Pl. III. fig. 16, Pl. IV. fig. 23). The four pairs of provisional appendages are now fully established, and the embryo has increased in length till the head- and tail-lobes are nearly in contact; the dorsal region is, as a consequence, much reduced. Behind the somites which bear the provisional appendages the tail-lobe has given rise to at least six indistinct additional somites; the terminal end of the tail is much narrowed and is becoming more pointed. The swellings produced by the rudimentary ganglia, at the bases of the appendages, are further developed, and the median ventral furrow has increased both in depth and in width.

Balfour has given good figures and descriptions of the germinal layers during the formation of the appendages. The mesoderm is of especial interest at this time. Early in the protozonite stage it forms a continuous band, about as wide as the embryo, composed of a single layer of cells extending the whole length of the embryonic band. About the time the appendages begin to appear the mesoderm splits along the median ventral line, thus forming two parallel bands, which remain united, however, in the head and tail regions. The division of the mesoderm into lateral halves is followed by an increase in the thickness of the resulting bands, each of which becomes split into a somatic and a splanchnic layer. It is also at this stage that the mesoderm is divided by transverse constructions into somites, each of which contains a central lumen. I am unable to determine from my specimens whether its division into successive blocks precedes or follows the appearance of the lumen. In the growth of the appendages the somatic layer of the mesoderm accompanies the outgrowing ectoderm, and forms a continuous lining to its cavity.

During this period the ectoderm has also increased in thickness, but along the median ventral line it remains thinner; from this it results that there are two bands of thickened ectoderm corresponding to the two deep bands of mesoderm. The ventral median depression previously mentioned is at first due to the relative thinness of the ectoderm in this region; it is afterwards made more conspicuous by the further separation of the mesodermic bands. From the ectodermic bands are formed the nervous ganglia. They are developed first in the thoracic region in the form of swellings at the bases of the appendages, but by the time the stage represented in Fig. 8 has been reached, they have also been formed in the abdominal region.

As already correctly maintained by Balfour, the segment of the cheli-



ceræ has a separate pair of ganglia which ultimately disappear, serving only to aid in the formation of the circumœsophageal commissure. At an early stage, then, the nervous elements consist of two rows of ganglia, a pair of ganglia for each somite, which are widely separated except in the head lobe and the tail lobe, where they are continuous in the median line.

Another important growth on the part of the ectoderm leads to the formation of the stomodæum, which arises as a simple tubular infolding between the ganglionic thickenings of the cheliceral somites, and immediately below the ventral margin of the cephalic plate. It becomes expanded at its deep end into a sort of pocket, but it has only a small external opening. The walls of the stomodæum are composed of cells, two or three rows deep, which are elongated and somewhat wedge-shaped rather than distinctly columnar.

4. The *period of reversion* is marked by the origin of many important organs: proctodæum, heart, lungs, tracheæ, spinning glands, muscles, etc. The embryo undergoes great changes in external form, gradually passing from the condition represented in Pl. II. fig. 8, where the ventral surface of the embryo is uniformly convex, and occupies an arc of about 300°, to a form (Pl. II. fig. 11) in which the ventral surface is folded upon itself.

As a prelude to reversion the tail-lobe of the embryo becomes prominent, being raised from the surface of the egg. The early steps in the process of reversion will be best understood from the examination of a series of dorsal views. Fig. 13 (Pl. III.) presents the dorsal aspect at the beginning of reversion, and Fig. 8 (Pl. II.) a side view at nearly the same stage. The tail-lobe has lost its broad rounded character, and is being changed into a more distinctively caudate structure. It still remains nearly in contact with the cephalic lobe. The dorsal elements ("terga" of Barrois) have begun their upward growth, and appear in the figure as four pairs of prominent lateral elevations. A corresponding growth of the abdominal segments is also in progress; the dorsal elements growing upward finally meet in the median line of the back.

Each of the lobes of the procephalic plate has a semilunar form, and is composed of a central area, apparently separated from a marginal rim by means of a deep fold (Pl. IV. fig. 23). The prominent upper lip (*lr.*) is apparently an outgrowth of the ventral border of the cephalic plate, and overhangs the entrance to the stomodæum (*s d.*).

The chelicerae (1 *app.*) and the pedipalpi (2 *app.*) both appear as post-oral structures. The prominent ganglia (*gn.*) belonging to the cheli-



ceral segment lie just in front of the bases of the chelicerae, and are likewise post-oral structures, as claimed by Balfour.

The next stage in the process is represented in Pl. III. fig. 14, in which the tail-lobe is much narrower and more clearly circumscribed; a considerable interval now separates it from the procephalic plate. Five pairs of dorsal (tergal) elements belonging to the abdominal segments are now visible; the four anterior pairs belong to the segments bearing provisional appendages, and a fifth, smaller pair, has been interpolated between these and the tail-lobe. The tail-lobe is apparently split in the median line into two bands that, in passing forwards, diverge rapidly. These are the two bands of ectoderm which, as before mentioned, join each other in the head and the tail-lobes. Between these divergent bands of ectoderm is to be seen a part of the yolk mass covered by only a thin layer of ectoderm. The legs have increased in length until they nearly meet in the median plane (Pl. IV. fig. 22).

In the next stage (Pl. III. fig. 15) the dorsal region is much elongated owing to the retrogression of the tail-lobe, and the rudimentary terga extend much further dorsad. Up to this time the only dorsal elements developed were the five pairs belonging to the abdominal somites, but during this stage the dorsal elements of the limb-bearing somites begin a more rapid growth. The dorsal elements of the somite bearing the fourth pair of legs grow much more rapidly than the others.

In a dorsal view of a somewhat later stage (Pl. III. fig. 16) the tip of the tail is just visible at the posterior margin of the embryo, the dorsal region having increased proportionately in extent. The procephalic lobes are closing together in the median plane. The dorsal elements of the somites now nearly meet in the median line of the back. In the figure some of the provisional appendages (*pr. app.*) are visible along the sides of the body.

In a slightly older embryo (Pl. III. fig. 17) the tail-lobe is no longer visible from above; the cephalic lobes have become fused, and the dorsal elements of the somites have met in the median line. Along this line a narrow slightly elevated ridge indicates externally the position of the heart.

The much reduced caudal lobe is to be seen from below (Pl. IV. fig. 21) and, diverging from it in two lines, the provisional appendages. Owing to the wide separation of the neural bands the legs of each pair are far apart. Between them a part of the yolk (not the whole, as stated by Barrois) protrudes, forming a sort of ventral yolk sack. The rapid appropriation of this store of yolk causes the disappearance of the sack;



the embryo becomes more folded upon itself ventrally, as shown in Pl. II. fig. 10, and the legs, increasing in length, gradually approach and finally overlap each other in the median line. The embryo has now acquired a strong ventral flexure — the reversion is completed.

During this period the bases of the chelicerae in growing have moved forwards and met in the median plane, so that they appear as pre-oral appendages. There has also appeared between their bases a prominent outgrowth to form the rostrum.

Balfour ('80, p. 180) endeavors to account for the process of reversion as the result of a rapid "elongation of the dorsal region, that is, the region on the dorsal surface between the anal and the procephalic lobes." I understand by this that it is to the growth of the ectodermic cells of the dorsal region that he would ascribe the elongation of the dorsal surface. I shall endeavor to show presently that this explanation is not sufficient to account for the changes which actually take place during reversion.

The growth of the derivatives from the ectoderm during the period under consideration is very great. At the beginning of the period the stomodæum forms a pocket-shaped invagination with a small external opening. Its calibre diminishes, except at its anterior end; it continues to grow inwardly, and at length forms an arched tubular organ, with its free end directed backward, and projecting some distance into the yolk. Near the close of the period its deep end becomes somewhat enlarged to form the rudiment of the sucking stomach. To the latter are attached a vertical muscle (*mu. vert.* Pl. IX. fig. 62) extending to the dorsal wall of the embryo, and two lateral muscles (*mu. lat.*).

The proctodæum is a later formation, which makes its appearance as an infolding at the tip of the tail-lobe some time after the beginning of this period. The relation of the tail-lobe to the rest of the body is best appreciated from sections, since it is not always evident from surface views that there is a deep fold which serves to separate it from the underlying portion of the dorsal surface. The prominence which it attains and the changes which it undergoes are readily traceable in a series of figures from successive stages during reversion (Pl. VIII. figs. 50-54). The strong resemblance of the condition shown in Fig. 50 to that which Bobretzky ('74, Fig. 15) has figured for *Oniscus* at an apparently similar stage of development, misled me into the supposition that I should find the proctodæum of *Agelena* developing in the manner described by him for *Oniscus*. But such is not the case. In *Agelena* the tip of the lobe is the tip of the tail — the morphological end of the body, and the depression which separates this lobe from the neighboring portion of the



embryo is not the proctodæum, but simply a fold in the dorsal wall of the embryo. The pocket resulting from this fold is flattened in a plane perpendicular to the sagittal plane, and is not a tubular infolding like the real proctodæum. This pocket is lined with ectodermic cells, which subsequently form a part of the epidermis at the posterior end of the dorsum. By the traction exerted along the median ventral line of the body during reversion the tail is drawn downwards and greatly shortened, thus obliterating the pocket. When in the progress of its reversion the embryo has reached about the stage represented in Figs. 10, 16, the proctodæum is formed as an invagination just ventral to its tip. At this early period it has the appearance shown in the sagittal section, Pl. VIII. fig. 54. The tail-lobe is now a short thick prominence, and the dorsal fold has nearly disappeared.

At an early period the proctodæum is enlarged by the outgrowth of its dorsal wall into the form of a capacious pocket, which is retained by the embryo throughout its development. This diverticulum (*br. stc.* Pl. VIII. figs. 55, 56) is the so-called stercoral pocket of the adult. The walls of the rectum and the stercoral pocket are composed of columnar epithelium, and are closely invested by mesodermic elements.

The nervous system is characterized during this period by the wide separation of the nerve bands and a gradual concentration of their substance headwards. The distance between the bands is greatly increased by the passage of the yolk from the dorsal to the ventral side through the aperture left by their separation. At the period of their greatest separation they occupy curved lines along the lateral walls of the yolk sack, separated from each other by its diameter. During reversion also the actual length of the nerve cords is somewhat decreased. At the beginning of this period they reach nearly around the egg from the head to the tail-lobe (Pl. XII. fig. 77), but during reversion they pass through the stages of shortening represented in Pls. XI. XII. figs. 72, 71, 70, 78. Their connection with the tail-lobe is severed, and the nerve cords gradually move forwards; with the absorption of the yolk mass this lateral separation is diminished until they are in contact along the ventral line.

After the process of reversion is well advanced certain cells in the bases of the chelicerae become conspicuous from their enlarged condition and spongy appearance, which serve to distinguish them sharply from surrounding cells. They are the rudiments of the poison glands, and although I have not been able to trace an external outlet until a later period, it is probable that these cells are derived from an infolding of the ectoderm at the point where later an outlet is discernible.



The spinning glands are not yet definitely established, but in the anal region on the ventral side of the proctodæum there is a large accumulation of ectodermic cells (Pl. XI. fig. 70) from which they are subsequently developed.

Late in this period the infoldings for the lungs arise. There appear a pair of large oval masses of cells, the nuclei of which are arranged in parallel lines (Pl. XI. fig. 73). From these cells the respiratory lamellæ of the lungs are finally formed.

The mesoderm likewise has been growing rapidly during reversion. In the previous period it was confined to the ventral portion of the embryo, but during the present period it grows upward on either side until it reaches the dorsal median line, thus forming a continuous layer beneath the ectoderm, as well as an investment for all organs, which arise as outgrowths of either ectoderm or entoderm.

The dorsal growth of the rudimentary terga, already spoken of as external features, is followed by this underlying layer of mesoderm. Early in the formation of the dorsal elements this mesodermic layer is divided into corresponding somites. Balfour ('80, p. 181) concluded that the cells out of which are formed the dorsal somites of the mesoderm "are not derived from prolongations of the somatic and splanchnic layers of the already formed [ventral] somites, but are new formations derived from the yolk." My sections, however, indicate that there is a direct continuity between the two (Pl. IX. figs. 59, 61), and that the dorsal mesoderm is an outgrowth from the previously established ventral mesodermic somites.

It is during this period also that the heart is formed. While I have been unable to arrive at an entirely satisfactory understanding of the details of its formation, I am convinced that it is not, as Balfour states, developed from a solid cord of cells, but from the dorsal limb of the up-growing mesoderm, and that its dorsal wall is closed first, while the ventral wall—the floor—remains for a time widely open below, thus communicating freely with the yolk. My sections also show that at a later period the aorta is formed, by means of a constriction, from the mesenteron. This agrees with the recent observations of Schimkewitsch, ('84\*).

A layer of characteristic cells, to which Balfour alludes in speaking of the formation of the dorsal mesoblast, precedes the formation of the heart in the dorsal region. These are what have been called "primary entoderm" cells, and are sharply distinguished from the surrounding cells by their large size, their large, oval nuclei, and their yellowish tint. These



cells are derivatives from the yolk-cells, and first appear just before the reversion of the embryo begins. They are abundant along the sides of the body, and about the œsophagus as well as in the dorsal region.

The yolk during this period is somewhat changed from its early characteristics. The corpuscles are undergoing disintegration, and are much vacuolated, which gives them in certain regions a spongy appearance. The nuclei of the yolk-cells, while they have increased in number, are smaller and angular (often triangular) in outline.

5. *The period from reversion to hatching.* — Few surface changes of importance are necessary to convert the embryo of the period just described into the adult. The following are the most obvious: The embryo becomes more closely flexed upon itself (Pl. II. fig. 11), and the constriction which separates the abdomen and the cephalo-thorax is formed. At least two pairs of provisional appendages are modified into as many large spinning mammillæ.\* In addition to these two large pairs there is a pair of smaller median mammillæ, the origin of which I have not traced. The remnant of the tail persists for some time as a post-anal knob; upon the ventral surface appear the infoldings, from which are formed the tracheæ, and also those of the generative organs; upon the head the eyes make their appearance. Two or three days before hatching the embryo begins to unroll, and undergoes a moult; at the time of hatching it is completely straightened.

I shall now proceed, after this general account of the more important embryonic stages, to the consideration of the development of separate organs and sets of organs.

### III. — Organogeny.

In the present paper only the following organs will receive attention: (1) the alimentary tract, including stomodæum, pharynx, stomach, mid-intestine, stercoral pocket and rectum; (2) the eyes; and (3) the lungs.

\* Balfour ('80, p. 183) has stated: "The four rudimentary appendages have disappeared, unless, which seems to me in the highest degree improbable, they remain as the spinning mammillæ." Notwithstanding his doubt, I think I have traced the development of two pairs directly into the mammillæ. The mammillæ, therefore, are appendages of abdominal somites, homodynamic with the cephalo-thoracic appendages, and there are consequently six somites condensed into the space between the posterior pair of mammillæ and the anus. Upon the ventral face the evidences of this are early obliterated, but upon the dorsal surface the posterior somites are recognizable by the arrangement of the longitudinal muscles, at least as late as the stage represented in Fig. 70, Pl. XI.



The portion of *the alimentary canal* first to appear — the stomodæum — arises as an invagination of ectoderm just before the beginning of the third period of development, and therefore after the establishment of a mesodermic layer in the region in which the invagination occurs. As already stated, it grows rapidly during the third period, and in the fourth period it acquires certain muscular attachments, developed out of mesodermic cells. After the reversion of the embryo is completed, a tube of about the same calibre as the stomodæum arises behind the stomach, and, extending through the cephalothorax, opens widely, by a bell-shaped expansion, into the yolk of the abdomen (Pl. XII. fig. 78). This post-gastric portion of the canal was evidently overlooked by Balfour, as he (l. c., p. 187) states that he was unable to find “any trace of an anterior part of the mesenteron adjoining the stomodæum.” Anteriorly it apparently does not open into the sucking stomach during embryonic stages, but is so plugged with cells that its relations are obscured.

At the time of hatching the intestinal tract is still incomplete, the epithelial wall of the mesenteron being largely or altogether wanting. There may be distinguished in the anterior portion of the tract the following parts: pharynx, œsophagus, sucking stomach, and post-gastric tube.

The pharynx passes from the mouth obliquely upwards and backwards, and, turning at nearly a right angle, is continued into the œsophagus. The latter is of uniform calibre and extends backwards with a slightly downward curve, terminating in the enlarged sucking stomach. A muscle arising from the dorsal wall of the cephalothorax just in front of the anterior margin of the brain, is inserted at the angle of the pharynx (Pl. XI. fig. 70, *mu.*). From the sucking stomach three distinct muscles extend to the body wall: a vertical muscle (*mu. vert.*), lying in the sagittal plane and extending downward from the cephalothorax a little behind the brain to be inserted along the dorsal wall of the stomach; a pair of lateral muscles (*mu. lat.*), which arise from the sternal plate and ascend obliquely towards the sagittal plane to be inserted into the lower half of the lateral walls of the stomach (Pl. IX. fig. 62; Pl. XI. fig. 70). A few fibres arising with the vertical muscle join the fibres of the lateral muscles without having a distinct attachment to the stomach (Fig. 62).

I am in doubt concerning the origin of the post-gastric tube already alluded to. Its anterior end, which lies just beneath the stomach (Pl. XII. fig. 78), is rounded and plugged with cells, and I have been able to trace an enveloping layer of mesodermic elements nearly across



its anterior surface. These facts afford strong evidence that this portion of the alimentary tract is derived from the entoderm rather than from the stomodæal infolding of the ectoderm. The cellular elements of which it is composed do not, however, differ enough from those of the stomodæum to add anything to the reasons just given for supposing an entodermic origin. But if, as I believe, this is not an outgrowth of the stomodæum, it must be the first-formed portion of the mesenteron, the walls of which, as we shall subsequently see, are begun at both ends and completed by the gradual advance and ultimate meeting of the two separate formations.

On each side of the stomach are given off cæca, which extend into the bases of the limbs. The cellular elements composing the walls of these tubes are flattened.

The walls of the anterior or stomodæal portion of the alimentary canal are composed of three layers: the cuticular, the epithelial, and the peritoneal. The pharynx, the œsophagus, and the sucking stomach are all lined with a cuticular layer which is continuous at the mouth with the cuticular covering of the body. In the pharynx it is thickened and corrugated by tooth-like projections, but in the œsophagus and the stomach it is much thinner and not roughened. I have not been able to make out satisfactorily whether this layer extends into the post-gastric portion or not. If it does, this would be an argument in favor of the ectodermic origin of this portion of the canal.

The posterior part of the alimentary canal — the proctodæum — does not begin until the reversion of the embryo is well advanced. Its external orifice is minute and leads directly into an expanded portion, which becomes the stercoral pocket. This enlargement is present at an early stage of the invagination, and presents in sagittal section a triangular outline (Pl. VIII. fig. 54). Its walls are at this time thick and composed of large ectodermic cells, which are, however, only a single layer deep. The invagination forming the proctodæum pushes before it an enveloping layer of the already formed mesoderm. The invagination is gradually differentiated into two parts: a straight narrow tube (the terminal portion of the rectum), and the stercoral pocket. The wall of the proctodæum is composed of columnar epithelium, the large spherical nuclei of which are placed close to the inner ends of the cells, which almost meet, and thereby nearly obliterate the lumen of the tube. This epithelium is enveloped externally by the usual layer of flattened mesodermic cells. The stercoral pocket increases rapidly in size, and becomes pear-shaped in outline. The cellular elements of its walls change from a columnar to a flattened epithelium. At the time of hatching its wall is



composed of three layers: an internal epithelial layer, composed of the flattened ectodermic cells with oval nuclei; a middle layer, composed of very much flattened cells, recognizable only by their long very narrow nuclei; and an external covering of mesodermic elements (Pl. IX. fig. 57).

A few days before hatching a short tube is to be seen extending forwards from the ventral face of the stercoral pocket to which it is joined. It is continuous behind with the part of the proctodæum which I have called the rectum, and in front it spreads out into a trumpet-shaped expansion which embraces the posterior portion of the yolk mass (Pl. VIII. figs. 55, 56; Pl. XI. fig. 70). The cells composing the epithelial lining of this portion of the intestine resemble more those of the stercoral pocket than those of the rectum. They are invested externally by a layer of flattened mesodermic elements continuous behind with those which envelop the stercoral pocket and the rectum, and in front with the mesodermic layer which invests the yolk.

Schimkewitsch claims for the hind part of the alimentary canal in *Epeira* a very thin cuticular lining; I have not been able to demonstrate its presence in sections of *Agelena*.

From the dorsal wall of the pre-stercoral tube — just where it becomes confluent with the antero-inferior face of the stercoral pocket — the two malpighian tubes take their origin. The position of these tubes furnishes the only evidence that I have concerning the source of the pre-stercoral tube, and leads to the conclusion that it is of entodermic origin, and therefore a part of the mesenteron.

I have not as yet traced the alimentary canal to its adult condition. At the time of hatching it is still incomplete, being composed of an anterior and a posterior portion, the inner extremities of which open towards each other by wide expansions, which abut directly upon the yolk. In the latest developmental condition that I have examined — about eight or ten days after hatching — the mesenteron is greatly extended, and appears to be continuous at its sides with the yolk compartments of the abdomen. It doubtless is functionally active previous to this time, since there was a considerable amount of effete matter in the stercoral pocket.

2. *The Eyes.* — It seems somewhat remarkable that up to the present time the development of the sense organs in the *Araneina* has been hardly more than touched upon. The meagre description by Claparède\*

\* Claparède ('62, pp. 56, 67) is the only one, I believe, who has written anything about the development of the eyes, and he has given only an account of the exter-



of the external features in the development of the eyes is, I believe, all that has been published upon that subject. I have been able, by means of sections, to trace the formation of the eyes, which begins at a comparatively late stage of development, through the most important changes. I shall confine my descriptions at first to the *median anterior* pair, which differ in some important respects from the remaining three pairs. The first step in their formation consists in local thickenings of the "hypodermis" (ectoderm) in the frontal region. Each thickening at first causes the deep surface of the hypodermis to bulge, while the outer surface retains its original direction. The thickening is soon followed by an extensive invagination, which begins just in front of the thickened

nal appearances in the region where the eyes are developed. Relative to Pholcus, he says (l. c., p. 56): "Les yeux n'apparaissent qu'à la fin de la vie embryonnaire, plus tard dans tous les cas que chez les Acarides, si j'en juge par les observations de Mr. Van Beneden sur l'*Atax Ypsilophora*. Leur apparition est précédée par la formation de quatre petits sillons que j'appellerai les sillons ophthalmiques. Les quatre sillons sont disposés par paires, deux d'entre eux appartenant au côté droit et deux au côté gauche. Ce sont de petites dépressions transversales, arquées, dont la convexité est dorsale. Les deux sillons de chaque côté vont en divergeant du côté externe. Ils répondent à la double rangée de yeux des Pholques. Avant que les yeux eux-mêmes apparaissent sous la forme de petits globes dans les sillons ophthalmiques, ceux-ci se colorent par le dépôt d'une petite quantité de pigment (v. fig. 25 en o)."

With regard to the formation of the eyes in *Lycosa*, he adds, (l. c., pp. 67, 68): "De même que chez les Pholques, nous voyons chez les Lycoses, les yeux n'apparaître que fort tard. Les pieds et les palpes ont déjà une grande partie de leurs articulations, lorsque les sillons ophthalmiques, au nombre de six, formant deux groupes symétriques de trois, se montrent comme précurseurs des yeux. Ces sillons ne tardent pas à se colorer par le dépôt d'un pigment sombre (fig. 45, Pl. V. en o). Plus tard le pigment, qui devient d'un noir rougeâtre, se groupe dans les sillons ophthalmiques en masses distinctes qui font légèrement saillie à la surface de la tête. De chaque côté de la tête deux de ces amas de pigment plus petits que les autres appartiennent au sillon inférieur, un appartient au sillon médian, un au sillon supérieur. Les huit yeux de l'araignée se montrent donc dans l'origine sous la forme de simples amas pigmentaires. Toutefois à l'époque où la Lycose quitte l'œuf, on aperçoit déjà au sein de chacun de ces amas de pigment un corps réfringent, le cristallin, sur la formation duquel je n'ai rien pu constater de précis. Ces yeux offrent alors la disposition indiquée dans la figure 50 (Pl. VI), disposition qui s'éloigne encore notablement de celle de l'adulte (v. fig. 51). Les quatre yeux de la rangée inférieure sont, au moment de la naissance, beaucoup plus petits que les autres. Ils le restent d'ailleurs toute la vie durant. Ceux de la ligne médiane sont les plus gros. On reconnaît facilement, tout au moins pour les quatre gros yeux, que chaque globe oculaire est pyriforme, se terminant en une pointe qui regarde l'arrière. Sans doute cette pointe n'est que l'extrémité périphérique du nerf optique, dont je n'ai pu cependant suivre le cours jusqu'au centre nerveux."



area. By this process of infolding the whole region of the thickening becomes inverted, and finally lies under that portion of the still unmodified hypodermis, which was at first just behind the thickening (Pl. X. figs. 63, 64), so that what was its external surface becomes its deep surface, and what was the deep surface lies relatively nearer the exterior. As a result of this infolding the region of the eye at this stage is composed of three distinct layers: an external (Figs. 64, 66, *h d*), a middle (*rtn'*) and internal (*rtn''*) layer. The external portion is composed of a single layer of cells, which at the outset do not differ from the hypodermis cells, with which they are continuous. The middle layer is the originally thickened portion, and is composed of elongated cells, all having the same general inclination; their nuclei are oval, being elongated in the direction of the long axis of the cells, and are arranged in three or four superimposed irregular rows. The internal layer, like the outer one, is composed of a single row of cells.

The pocket of the invagination is not very broad, as is best to be seen on frontal sections (Pl. X. fig. 65). After a time the orifice of the invagination is closed by a fusion of its lips, and the retinal bulb, formed by the middle and internal layers, becomes separated from the hypodermis; thus all direct evidence of its mode of origin is obliterated.

After the invagination is completed the cells of the external layer begin to elongate; they are now so closely crowded together that their nuclei are almost in contact, and the cell boundaries are not easily distinguishable. Their nuclei also become lengthened, without losing much in thickness, until they are three or four times as long as broad. An accumulation of homogeneous faintly stainable substance appears between the thin cuticula, which everywhere covers the hypodermis, and the free ends of these elongated cells; it is not at first sharply defined from the latter (Pl. X. fig. 66). This accumulation of substance finally causes an elevation of the surface, and just before hatching it has assumed a tolerably lenticular shape (Pl. X. fig. 68, *lns.*). It gradually becomes more refractive, and a few days after hatching assumes nearly the form of the cuticular lens of the adult (Pl. X. fig. 69, *lns.*). The lens is evidently produced by the secretive activity of the underlying elongated cells; these have, in the meantime, continued to elongate, and their boundaries have become sharply defined; during this period the nuclei do not seem to share in the process of elongation, for after the formation of the lens they are seen to occupy the deep ends of the cells, and to be only a little larger than the nuclei of the adjacent hypodermis (Pl. X. fig. 69, *h d*). This layer of cells now constitutes the so-called



vitreous body of the eye, and is, as just shown, a modified portion of the hypodermis, with which it has never ceased to be continuous.

The cells of the middle (inverted) layer undoubtedly form all of the retinal elements. I am unable to assert positively what becomes of the "inner layer." Certain stages show that the nuclei of this layer have become considerably flattened in the direction of radii to the optic bulb, so that it is possible they ultimately constitute a kind of enveloping tunic to the deep surface of the bulb. That I have not mistaken mesodermic elements for this posterior layer, is evident from the great size of the nuclei, and the successive stages exhibited in the conditions of the layer. It, therefore, seems to me at present doubtful if the inner layer really shares in the formation of the retina proper. After the completion of the infolding the cells of the middle layer elongate and the layer thus becomes thicker, especially its central portion, and the whole invaginated mass, therefore, assumes a more nearly spherical form. This elongation of the cells appears to result from an outgrowth of their anterior ends, since the nuclei are crowded into the deeper portions of the layer, while the anterior part becomes translucent. The formation of the bacilli in the extreme anterior ends of the cells soon makes this part of the layer more highly refractive. The bacilli increase in length from before backwards. A little later a zone of pigment granules makes its appearance in the retinal cells between the forming bacilli and the more anterior of the nuclei. These granules are limited to near the surfaces of the cells. About the same time a layer of pigment cells is observable along the deep surface of the eye-bulb. They are probably the cells of the "inner layer" of the involution, for they do not appear to be elongated in the direction of the axis of the bulb, as are the nuclei of the true retinal or nerve-end cells. As the pigmentation increases it appears in some of the retinal cells in a position posterior to the prenuclear zone above mentioned; these patches of pigment seem to correspond in height with the elongated nuclei of the cells, and are not always continuous with the prenuclear zone of pigment.

It is probable, therefore, that not only the posterior ends of the bacilli are practically ensheathed by a layer of pigment, but also that the nuclei of the nerve-end cells become more or less enveloped in pigment, and that the two zones are not at first continuous with each other, nor with the still more posterior pigmentation of the inner layer. The pigment in all cases belongs to cells of the originally involuted ectoderm, and there are no interstitial cells between the nerve-end cells of the retina; at least satisfactorily stained specimens show only nuclei of two sorts: namely,



the large elongated nuclei of the nerve-end cells and the flattened nuclei of the inner layer. In this stage (Pl. X. fig. 69) the essential features of the eye are established, and it is possible to affirm positively that the anterior median eyes in *Agelena naevia* belong to the type in which the nuclei of the retinal cells are *post-bacillar*.

The three remaining pairs of eyes originate somewhat later, but in substantially the same way as the pair just described; a hypodermic thickening, a backward directed infolding which inverts the thickened region and carries in beneath it a thin layer of hypodermis, the closure of the orifice of involution, and the detachment of the involuted mass from the hypoderm. The lens is also produced from modified hypodermic cells resembling, though shorter than, those forming the lens of the median anterior pair. But the two layers of the infolded mass do not undergo the same changes as do the corresponding layers in the pair of eyes previously described. In the first place, the two layers remain permanently (up to my latest stage, ten days after hatching) separated by the development of a (in hardened specimens) much folded chitinous layer, which is probably homologous with the cuticular covering of the body, with which in the earlier stages it appears to be continuous. Secondly, while the retina is developed as in the anterior eyes, from the cells of the *inverted* portion of the infolded region, the bacilli do not arise in the ends of the cells which adjoin the vitreous body, but at the opposite or posterior ends. They are, therefore, found in the immediate vicinity of the chitinous substance. The nuclei, in the latest stages examined, still continue to occupy the anterior portion of the layer. Whether they are ultimately displaced to the margin of the retina, I am not at present able to say. Clearly, however, the retina is developed out of the middle layer, as in the previous case, but the nuclei of the retinal cells are *pre-bacillar* in position. About the time of hatching nerve filaments grow out from the brain, and thus connect the cerebral ganglia with the retinal portion of the eye.

3. *The lungs* arise as a pair of extensive invaginations at about the same time as the proctodæum. In sagittal sections of early stages the lungs appear as oblong plates of cells, the large oval nuclei of which are arranged in parallel rows (Pl. XI. fig. 73). The cells forming the ventral wall of the floor over the lung sacks, however, are several layers deep, and their nuclei are not arranged in parallel rows as the other nuclei are. The nuclei of the parallel rows undergo a change of form, becoming flattened on one side and very convex on the other. In each single row the convex faces look in the same direction, but the rows are



so arranged in pairs that the convex surfaces of all of the nuclei in one row are directly opposite the convex surfaces of the same number of nuclei of an adjacent row. The cells whose nuclei constitute such a pair of rows form the two walls of a thin flat hollow sack, a respiratory lamella. The outer surface of each lamella is covered with a continuous thin chitinous secretion from these cells. The flattened surfaces of the nuclei are turned outwards as regards the lumen of the sack, and the convex faces are turned inwards. Ultimately the cells corresponding to each pair of nuclei, which thus face each other, come in contact, and are apparently fused together, thus forming pillars of protoplasmic substance joining the walls of the lamella. The posterior borders of the lamellæ are free, and in most of the sections a pair of these cells with large nuclei are found at these free ends. In the later stages (six or eight days after hatching) the marginal pairs of cells become pigmented like the "hypodermis" cells generally. The other cells remain up to this time without pigment.

The surface of each lamella presents, as has been said, two chitinous limiting membranes, one forming its dorsal surface, the other its ventral surface; these are continuous with each other at the free (posterior) rounded margins of the lamellæ, and at their anterior limit with the corresponding membranes of the lamella next above and below, respectively. There is a constant difference between these chitinous coverings: that of the ventral surface is smooth and of uniform thickness, that of the dorsal surface is early characterized in sagittal sections by the presence of fine, close-set faintly expressed tooth-like markings. These markings may be traced over the free edge of the lamella, but do not extend on to its ventral surface.

The space embraced between the two chitinous layers of each lamella is interrupted at intervals by the short 2-cell columns described above, each with a single nucleus, which is so large as to touch its neighbor. The protoplasm enveloping the nuclei is exceedingly scanty, and thins out at the flat margins of the nuclei into a layer which it is difficult to trace as a lining to the chitinous membrane. It occasionally presents slight irregular elevations, which project into the common cavity. Through the anterior attachments of the lamellæ, the cavities of which communicate directly with the body-cavity, the blood has free access to the cavity of each respiratory lamella; blood corpuscles are consequently to be seen in sections (Pl. XII. fig. 76, *cp. hæ.*), and the coagulated plasma of the blood often fills the lamellar cavities more or less completely.



While these changes in the cells composing the lamellæ have been taking place, those which form the ventral wall of the body covering the lungs have become definitely arranged in two layers — an outer one, which is distinctly continuous with the hypodermis of the surrounding regions of the body, and like it is composed of a single layer of close-set pigmented cells, with large elongated nuclei, and a deeper one composed of elongated, unpigmented cells, with smaller nuclei. These two layers are continuous with each other at the anterior lip of the pulmonary opening.

The two layers of cells are connected by cellular strands, probably of a muscular nature, which run obliquely downwards and forwards from the inner to the outer layer. They appear to be simple elongations of the body of the cells of the inner layer. The remaining space between these two layers forms a part of the body cavity, and like the true lamellæ is traversed by the blood. The dorsal chitinous covering of the inner layer is toothed like the dorsal surface of the true lamellæ. According to the figures of the adult structure given by MacLeod ('84, Pl. I. fig. 3), one would expect to find the chitinous layer of this surface plain rather than complicated.

I have not yet succeeded in demonstrating the existence of any muscular differentiations in the 2-cell columns, such as is described and figured by MacLeod for the adult.

#### IV.—General Considerations relative to some of the Phenomena.

The discussion concerning the nature of the peripheral layer of protoplasm — or *blastema* — in the early condition of the laid egg, has already been referred to. Sabatier ('81) is the only author who has attempted to assign a cause for the division of this layer into definite polygonal areas. He concluded that the cause resides in the movements of the internal protoplasm which migrates towards the periphery. This hyaline protoplasm gushing forth from between the yolk corpuscles at the surface produces, in his opinion, certain lines of division in the blastema. The areas thus formed naturally correspond in size and position with the yolk corpuscles.

In view of the facts learned from sections of this stage this explanation seems to me inadequate. If the markings were produced by a centrifugally directed force the dividing lines would be at least "flush" with the surface of the blastema, if not slightly elevated above it. As a matter



of fact they are depressed (Pl. V. fig. 28 ; Pl. VI. fig. 30), and, therefore, can be accounted for more reasonably on the supposition of a centripetal force. It has already been indicated that these areas are formed during the contraction of the vitellus ; surface views and sections combined show that the very plastic protoplasm of the blastema is moulded to the surface of the peripheral yolk corpuscles, to which it at first forms caps, all of the caps being joined at their margins. Owing to mutual pressure these subsequently appear as polygonal areas. The cause, then, producing this surface phenomenon is mechanical, and depends upon the contraction of the protoplasm of the egg. But under what influence does this contraction transpire? As the phenomenon takes place during the stage which is characterized by the existence of the first segmentation-nucleus, it is more than probable that the cause is resident in this central nucleus, which exerts its attractive influence on all the protoplasm of the egg, but finds its external manifestation at this period principally in the blastema. Thus, it is probable that the same cause which produces in these eggs contraction of the vitellus, also induces the division of the blastema into areas.

The manner in which the protoplasm acts upon the yolk in the assimilation of its substance is clearly indicated in the blastema stage. That portion of the surface of the corpuscles which is in contact with the protoplasm of the blastema appears deeply eroded (Pl. VI. figs. 30-33), and the fine fragments into which the detached yolk substance is broken gradually merge into the still more finely granular protoplasm. A somewhat similar fate overtakes the yolk corpuscles in the vicinity of the central nuclei (Pl. V. figs. 28, 29 ; Pl. VI. fig. 34). Here, however, there is a very gradual transition from the larger corpuscles to the much smaller ones which immediately surround the finely granular protoplasm of these central cells, — a process of fragmentation appears to precede the erosion, and thereby a much greater surface of yolk substance is exposed to the action of the protoplasm. In the former case there is no total fragmentation of the yolk corpuscles, and the erosion proceeds from one side only, leaving the opposite side with a sharp, more or less even outline. The preliminary fragmentation of the yolk in the vicinity of the rapidly proliferating cells is, without question, correlated with the rapid growth of the latter.

Claparède ('62), Barrois ('78), and Balfour ('80), have each given explanations of the *reversion of the embryo*. Balfour's is the simplest.



According to his conclusions the reversion is produced by the longitudinal expansion of the dorsal region. It should be borne in mind that previous to reversion the ventral plate extends nearly around the egg, bringing the head end and the tail end near together on the dorsal side, and that the narrow region separating these two structures represents properly the whole of the dorsum. By expansion of the dorsum the head and tail are removed further and further apart, and, according to his notion, the embryo naturally bends upon itself ventrally, since it cannot straighten out, and since, as he erroneously states, it does not become shorter.

I have already shown (Pl. VIII. figs. 50-52) that the tail-lobe becomes separated from the rest of the body during reversion, a condition that has not hitherto been recognized, but which is very apparent in sagittal sections. This fact alone is sufficient to show that Balfour's explanation as stated is untenable, for were reversion produced by a simple expansion of the dorsal region, — unaccompanied by shortening of the embryo, — at the end of the process the tail would still exist as an elongated conical appendage, instead of being shortened almost to obliteration. In reality, however, a shortening of the ventral band does take place, which is at least equal to the pre-existing tail-fold, and the tail is in consequence drawn forward ventrally. This shortening would tend to make the bands assume the position which would make the distance between head and tail least. There are further to be accounted for in this period, the wide divarication of the nerve bands and the ventrad movement of the passive yolk mass. The cause for the latter must be found in the relative pressures exerted upon it by the dorsal area on the one hand and the ventral area on the other hand: that area which is increasing most rapidly in extent would exert a constantly diminishing pressure; however, the shape of the area is of the utmost importance. Although the dorsal region is changing its proportions most, it changes rapidly from a very *broad and short* condition to a *long and narrow* one. The principal force, then, that pulls the nerve bands away from the ventral surface is the one which tends to reduce the width (not as Balfour will, the one that increases the length) of the dorsal region. The evident cause for this reduction in width is the dorsad concentration of the ectodermic elements which accompanies the formation of the so-called terga, and this is also the cause for the descent of the yolk mass, for the cells that are brought close together to form the thickened ectoderm of the tergal region put the remaining cells of the dorsal region to a tension, the force of which is exerted upon the yolk mass. It will be remem-



bered that at this time the ventral area is composed of a thin layer of ectodermic cells; these cells offer the least resistance to the movement of the yolk mass, which, therefore, takes a ventrad direction.

During the period of reversion *Agelena* presents an interesting resemblance to certain conditions in the development of *Oniscus*. But according to Bobretzky ('74, Fig. 15, *hd.*) the proctodæum in *Oniscus* arises some time before the formation of a tail-fold (l. c., Fig. 17, *rf.*), which, moreover, is never conspicuously indicated. In *Agelena* the tail-lobe is very prominent, and the fold which results in its formation appears long before the proctodæal invagination. The appearance of this tail-fold, as seen in sagittal sections, is so like that presented by the first stage in the formation of the proctodæum in *Oniscus* (l. c., Fig. 15) as to suggest the possibility that the infolding in the latter case is really a tail-fold and not the proctodæum, in which event *hd.* of Fig. 15 would correspond to *rf.* of Fig. 16, and the proctodæum in the latter figure would be a new invagination. The principal objection to this view, aside from the author's reputation for accurate observation, lies in the closeness of the stages of Figs. 15 and 17, which would not seem to allow time for such radical changes. Another and perhaps sufficient objection is, that the invagination in question (*hd.* Fig. 15) is lined with columnar epithelium like the proctodæum of the succeeding stage, and that the slight tail-fold is lined with flat cells. But whatever may be the truth with regard to *Oniscus*, I am certain that in *Agelena* the tip of what I have called the tail-lobe becomes the morphological end of the body, and that the proctodæum pierces the tip of this lobe *after the reversion of the embryo is nearly completed*, and the tail-lobe has become much shortened.

One fundamental difference supposed to exist between the eyes of Arthropods and those of Vertebrates, relates to the direction in which the light traverses the retinal elements. In the vertebrate eye the light passes through the cells from their deep to their outer (genetically considered) ends. In the arthropod eye the light was supposed to have the reverse direction; but that this difference does not exist in the eyes of *Agelena* is rendered apparent from its manner of development already described. If the proliferation of cells which precedes the invagination led directly to the formation of the eyes, the light would then traverse the percipient elements from their outer to their deep ends; and it is probable that an ancestral eye of this kind prevailed. In the process of invagination, however, this thickened portion — from which are formed the retinal elements — is completely inverted, and as a consequence the



light must traverse the cells from their deep to their outer (genetically considered) ends. There is, therefore, a striking analogy between the condition which obtains in the eye of the spider and that which prevails in the case of all vertebrates.

SAINT CLOUD, MINN., Dec. 1, 1885.

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DESCRIPTIONS OF FIGURES.

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LIST OF ABBREVIATIONS.

A.	<i>an.</i>	anus.	L.	<i>lab.</i>	labium.
	<i>ao.</i>	aorta.		<i>lens.</i>	lens.
	1. <i>app.</i>	1st pair of appendages.		<i>lob. ca.</i>	caudal lobe.
	2. <i>app.</i>	2nd pair of appendages.		<i>lob. ce.</i>	cephalic lobe.
	6. <i>app.</i>	6th pair of appendages.		<i>lr.</i>	labrum.
B.	<i>b.</i>	brain.		<i>lu.</i>	lumen.
	<i>bl'.</i>	blastema.	M.	<i>ms d.</i>	mesoderm.
	<i>bl d.</i>	blastoderm.		<i>ms d. so.</i>	mesodermic somite.
	<i>br. stc.</i>	stercoral pocket.		<i>mu.</i>	muscle.
C.	<i>cd. ab.</i>	abdominal portion of nerve cord.		<i>mu. lat.</i>	lateral muscle.
	<i>cd. n.</i>	nerve cord.		<i>mu. vrt.</i>	vertical muscle.
	<i>c dn. ca.</i>	caudal thickening.	N.	<i>nl.</i>	nucleus.
	<i>ch.</i>	chorion.	O.	<i>æ.</i>	œsophagus.
	<i>cr.</i>	heart.		<i>ocl.</i>	ocellus.
	<i>cta.</i>	cuticula.	P.	<i>phx.</i>	pharynx.
	<i>cum. pr.</i>	primitive cumulus.		<i>p pl.</i>	protoplasm.
D.	<i>d.</i>	dorsum.		<i>pr. app.</i>	provisional appendages.
E.	<i>ec.</i>	ectoderm.		<i>pr d.</i>	proctodæum.
	<i>ed.</i>	epidermis.		<i>pr-stc.</i>	pre-stercoral tube.
	<i>en.</i>	large so-called ento- dermic cells.		<i>pr z.</i>	protozonite.
G.	<i>gl.</i>	gland.		<i>p-s d.</i>	post-gastric tube.
	<i>gl. src.</i>	spinning gland.	R.	<i>rtn'.</i>	1st (inverted) layer of op- tic invagination.
	<i>gn.</i>	ganglion.		<i>rtn''.</i>	2nd (non-inverted) layer.
	<i>gra.</i>	granular ("puncti- form") substance.	S.	<i>s d.</i>	stomodæum.
H.	<i>hd.</i>	hypodermis.	T.	<i>T.</i>	tail, tip of body.
I.	<i>iv.</i>	invagination, to form the pulmonary sac.		<i>trg.</i>	tergite.
			V.	<i>vit.</i>	"vitreous body."
				<i>vl.</i>	vacuole.
			Y.	<i>yk.</i>	yolk.

The figures of Plates I.-IV. are surface views of eggs by reflected light, each magnified about sixty diameters.

PLATE I.

Fig. 1. An egg showing the primitive cumulus.

" 2. A more advanced egg, showing the primitive cumulus, the caudal thickening (*c dn. ca.*), and between the two, traces of the forming ventral plate.



- Fig. 3. The same view of another egg.  
 " 4. End view of an egg at the stage of the primitive cumulus.  
 " 5. View upon the anterior end of the egg from which Fig. 2 was drawn.  
 The larger polygons are boundaries of yolk masses, the smaller those of blastoderm cells.

## PLATE II.

- Fig. 6-11 are *side views* of eggs, and are arranged in the order of their sequence in development.  
 " 6. Left side of the embryo at the stage which exhibits six protozonites.  
 " 7. View of the right side at the stage marked by the beginning of the appendages.  
 " 8. A more advanced embryo (left side) with incurved permanent appendages and four pairs of provisional appendages.  
 " 9. A somewhat oblique view of the right side during the period of reversion, showing the rudimentary terga (*trg.*), also an increase in the distance between the cephalic and caudal lobes.  
 " 10. Embryo (left side) when reversion is nearly completed, showing the persistence of the two posterior pairs of provisional appendages, and also their change in position to the posterior part of the body.  
 " 11. Embryo after the reversion is completed; the last two pairs of provisional appendages are being modified to form the spinning mammillæ.

## PLATE III.

- Fig. 12. The head and tail lobes at the stage when the appendages begin to appear.  
 " 13-17 form a series of *dorsal views* during reversion.  
 " 13. Dorsal view of an embryo at the beginning of reversion.  
 " 14. An embryo a little further advanced, to show the separation of the head- and the tail-lobes, and also the increase in the dorsal extension of the tergites.  
 " 15. A similar view of an embryo a few hours older than the preceding.  
 " 16. Dorsal aspect of a still older embryo, in which the tail-lobe is just disappearing from the dorsal surface.  
 " 17. An embryo at about the stage represented in Fig. 11.

## PLATE IV.

- Fig. 18-23 present a series of *ventral aspects*.  
 " 18. An embryo at the stage which shows six protozonites.  
 " 19. An embryo showing the beginning of the appendages; it is of the same age as that shown in Fig. 7.  
 " 20. View of the caudal lobe at about the same stage as is represented in Fig. 8.  
 " 21. Ventral view during the period of reversion. The embryo corresponds nearly with the stage represented in Figs. 10 and 16.  
 " 22. Ventral aspect of the embryo from which Fig. 14 was drawn.



- Fig. 23. An enlarged view of the head region, at about the same stage as the preceding.

## PLATE V.

- Fig. 24. A portion of the surface of a living egg of *Agelena naevia*, after the division of the blastema into polygonal areas. Several of the yolk corpuscles have shifted from their original positions, and therefore no longer coincide with the areas.  $\times 163$ .
- " 25. Polygonal areas of the blastema and underlying yolk globules more highly magnified; from a living egg.  $\times 440$ .
- " 26. Primary blastodermic cells before they become regular in form and size; from a living egg.  $\times 163$ .
- " 27. A portion of the blastoderm on the third day (temperature  $23^{\circ}\text{C}$ ) of development; from a living egg.  $\times 163$ .
- " 28. A little more than one half of the section of an egg, containing only one nucleus, the first segmentation nucleus; showing blastema (*bl'*), nucleus (*nl.*), and yolk corpuscles (*yk.*).  $\times 110$ .
- " 29. First segmentation-nucleus with the surrounding protoplasm highly magnified, showing also a rapid diminution in the size of the yolk corpuscles in its vicinity.  $\times 330$ .

## PLATE VI.

- Fig. 30. Enlarged view of a portion of Fig. 28, showing the blastema (*bl'*) and underlying yolk corpuscles (*yk.*).
- " 31, 32. Isolated peripheral yolk corpuscles, to which portions of the blastema are attached.
- " 33. Isolated yolk corpuscle with a vacuole, which in turn contains a rounded yolk globule.
- " 34. Section through the nuclei of an egg in the two-cell stage, showing the two groups of yolk columns (*Deutoplasmasäulen*).  $\times 110$ .
- " 35. One of the deep internal cells, surrounded by yolk.
- " 36. A nucleus containing a central vacuole; from an egg in the two-cell stage.
- " 37. A migrating cell that has just reached the periphery, abutting on the blastema (*bl'*).
- " 38. Detached portion of the blastema viewed from within, showing depressions into which the yolk corpuscles fit.
- " 39. Section of an egg passing transversely through the primitive cumulus in the region of its greatest width.  $\times 110$ .

## PLATE VII.

- Fig. 40. Radial section of two blastodermic cells.
- " 41. Section passing sagittally through the primitive cumulus.  $\times 110$ .
- " 42. A blastodermic cell in the process of division, with "interzonal filaments."



- Fig. 43, 46, 47. Blastodermic cells; to show some of the conditions presented by the chromatine and nucleoplasm of their nuclei.
- " 44. A cell in the process of division, further advanced than the one represented in Fig. 42.
- " 45. A portion of Fig. 49 highly magnified to show the columnar nature of the ectodermic cells and the complete differentiation of the mesoderm.
- " 48. Ectodermic cells with two nuclei from a late stage, during the infolding, to form the ovary.
- " 49. Sagittal section through an embryo in the protozonite stage,  $\times 110$ .  
Note. — In cutting and mounting, the section was artificially ruptured in two places, but none of the blastoderm has fallen away.

## PLATE VIII.

- Fig. 50. Sagittal section through an embryo during reversion, showing stomodæum, tail-lobe, etc.  $\times 110$ .
- " 51, 52. Views of sagittal sections of the posterior region during reversion, to show the condition of the tail-fold.
- " 53. Section of the tail region and a part of the dorsal region, to show the mesodermic somites of the rudimentary terga. The section is cut obliquely to the median plane.  $\times 110$ .
- " 54. Sagittal section of the morphological tip (*T*) of the body near the close of reversion, to show the early condition of the proctodæum.  $\times 110$ .
- " 55. Sagittal section of the hind part of the body, to show the stercoral pocket (*br. stc.*) and the pre-stercoral tube (*pr-stc.*).
- " 56. Sagittal section of the hind part of the body, to show the trumpet-shaped condition of the pre-stercoral tube and the somatization of the body as indicated by the segmental grouping of the muscles (*mu. 1 — mu. 5*).

## PLATE IX.

- Fig. 57. A nearly horizontal section of the proctodæum and the stercoral pocket (*br. stc.*), about three days before hatching, showing the columnar epithelium and the narrow lumen of the proctodæum.  $\times 310$ .
- " 58. Sagittal sections of anus and stercoral pocket, about eight days after hatching.  $\times 110$ .
- " 59. About one half of a transverse section in the region of the "rudimentary terga," to show the mesodermic somites of these dorsal elements and their connection with the ventral portion of the mesoderm.  $\times 100$ .
- " 60. Transverse section of an embryo near the beginning of reversion, passing through the stomodæum and the 2nd pairs of legs.  $\times 100$ . Compare the separated nerve bands (*gn.*) with those of Fig. 62.
- " 61. A section from the same embryo as Fig. 59, showing entodermic cells (*en.*) in the region of the tergal elements.
- " 62. Transverse section after completed reversion, through that part of the stomodæum which becomes the sucking stomach. It shows the muscles attached to sucking stomach (*mu. vrt.*, *mu. lat.*), and the approximation of the nervous bands (*gn.*).  $\times 110$ .



## PLATE X.

Sections illustrating the development of the eyes.

The four pairs of eyes are called according to their positions: anterior lateral, anterior median, posterior lateral, posterior median.

- Fig. 63. A sagittal section showing an early condition of an anterior median eye, — a thickened mass of "hypodermis" cells with the beginning of an invagination.  $\times 430$ .
- " 64. Sagittal section of an anterior median eye after the invagination is fully established, three or four days before hatching.  $\times 430$ .
- " 65. A frontal section through the anterior median pair of eyes, showing the narrow lumen of the invagination and its limited lateral extension.  $\times$  about 300.
- " 66. An older stage (one to two days before hatching) showing an elongation on the part of the "hypodermis" cells which constitute the "vitreous body," and also the closure of the invagination.  $\times 430$ .
- " 67. A sagittal section passing through an anterior and a posterior eye of the same side, two days after hatching.  $\times 430$ .
- " 68. Sagittal section through an anterior median eye one day before hatching.  $\times 430$ .
- " 69. Sagittal section through an anterior median eye, eight days after hatching; the retinal portion has not yet reached its full development.  $\times$  about 350.

## PLATE XI.

- Fig. 70-72, 77, 78, show the gradual headward concentration of the nerve bands. Fig. 77 represents the earliest stage, in which the nerve bands reach nearly around the egg; Fig. 72 shows the nervous elements contracted so as to occupy only the folded ventral region; in Fig. 71, the abdominal cord is shortened considerably more; Fig. 70 represents the ventral ganglia concentrated within the thorax; Fig. 78 shows the condition of the brain and ventral ganglia at the time of hatching.
- " 70. Sagittal section approximately in the median plane, from an embryo about two days before hatching.
- " 71. Sagittal section through the brain and nervous ganglia at about the completion of reversion.  $\times 110$ .
- " 72. Sagittal section through the nervous system at the stage of the formation of the proctodæum.  $\times 100$ .
- " 73-76 show four successive stages in the formation of the lungs, all magnified about 300 diameters.
- " 73. View of the right-hand surface of a sagittal section of the lungs in an early condition (about the middle of the period of reversion), showing the nuclei arranged in parallel rows.



## PLATE XII.

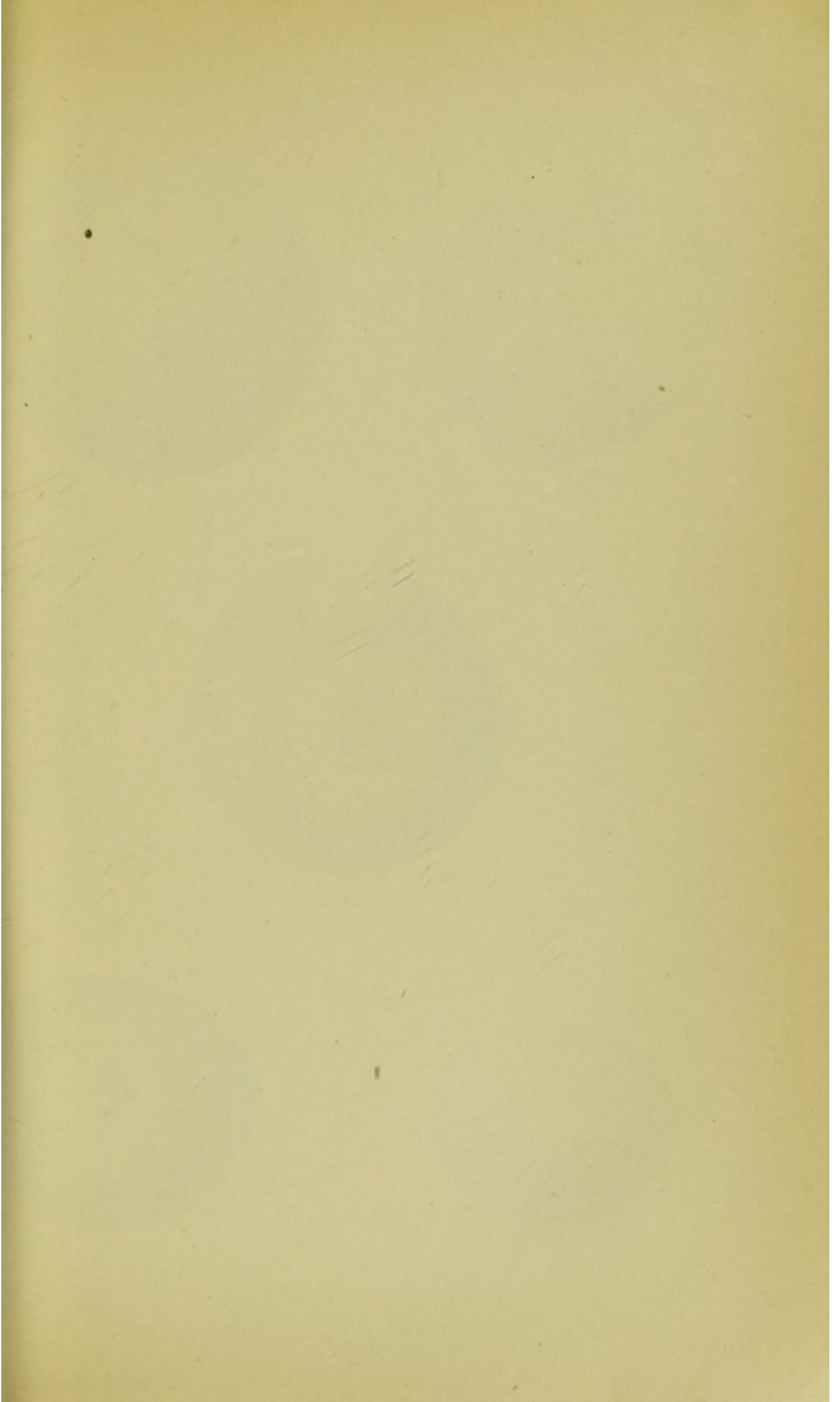
- Fig. 74. Sagittal section (left-hand surface) from an embryo somewhat older than the preceding.
- " 75. Sagittal section of the lungs at about the time of hatching.
- " 76. Sagittal section of the lungs five or six days after hatching; the upper and lower walls of each lamella are connected by the union of the nuclei (*nl.*).
- " 77. Sagittal section showing the nervous system at the beginning of reversion.
- " 78. Sagittal section of the cephalothorax at the time of hatching, to show the post-stomodæal portion of the alimentary canal, and also the concentrated condition of the ventral ganglionic mass.



PLATE XII

- 1. Sagittal section (Fig. 1) and another from an embryo showing the position of the pectoral girdle.
- 2. Sagittal section of the lungs at about the time of hatching.
- 3. Sagittal section of the lungs from an adult, showing the position of the pectoral girdle and the position of the lungs.
- 4. Sagittal section showing the nervous system at the beginning of hatching.
- 5. Sagittal section of the respiratory system at the time of hatching, to show the position of the respiratory system and the position of the pectoral girdle.
- 6. Sagittal section of the respiratory system and the position of the pectoral girdle.

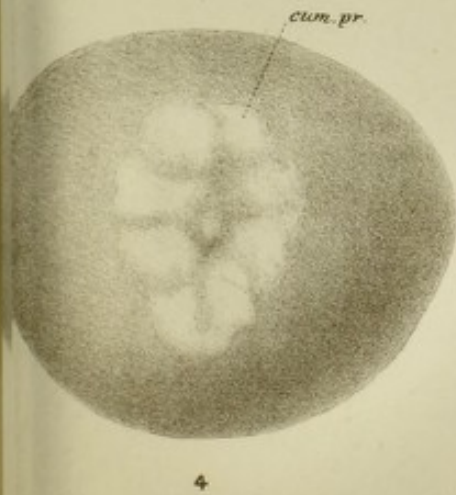
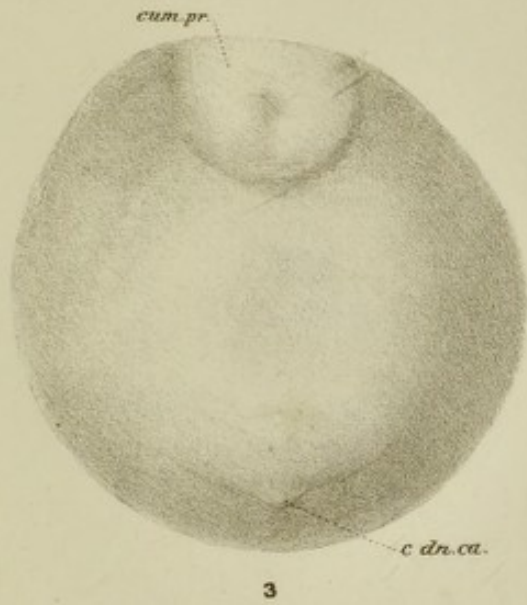
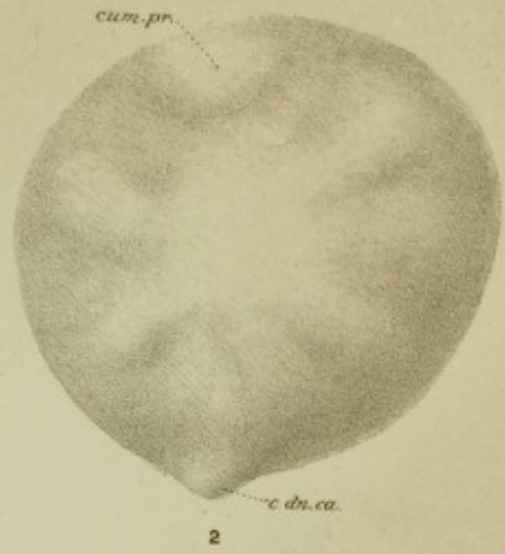
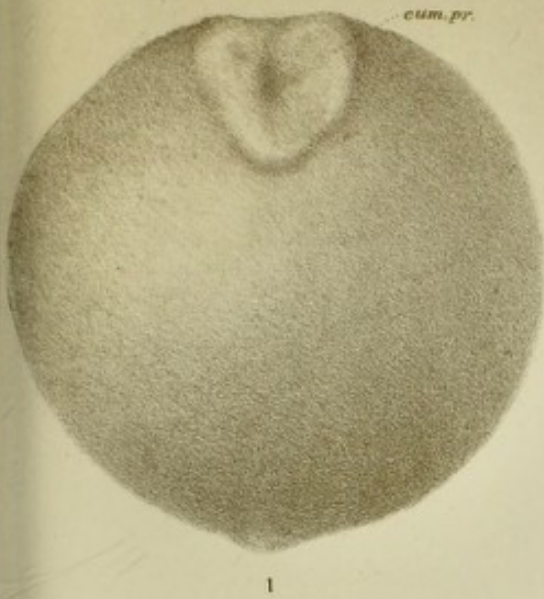












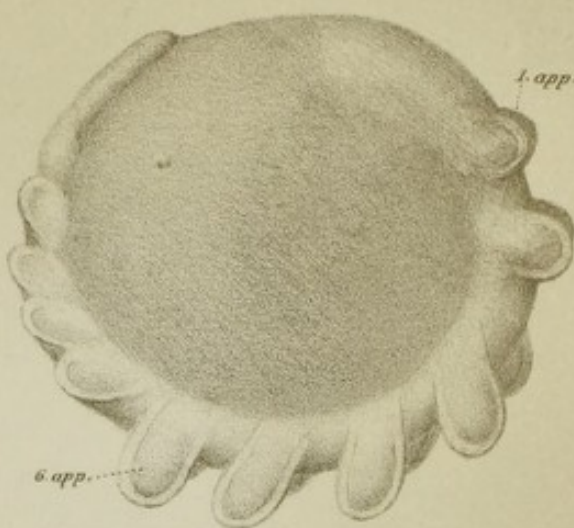




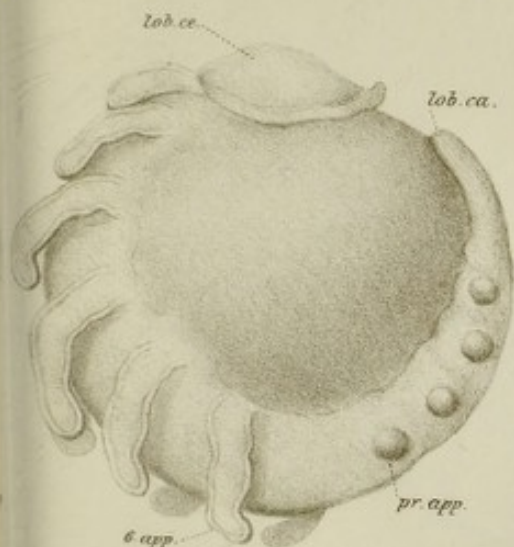




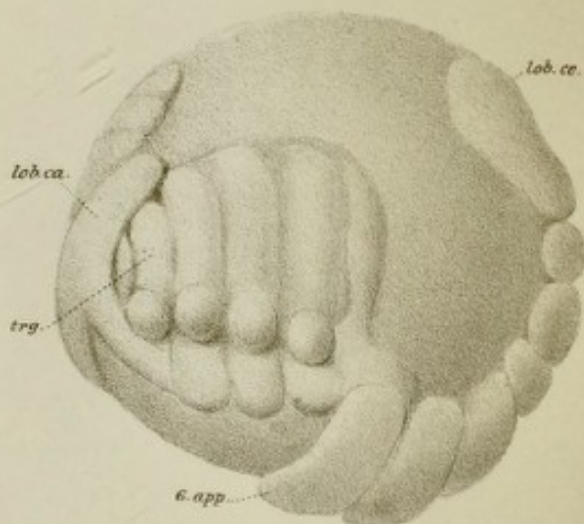
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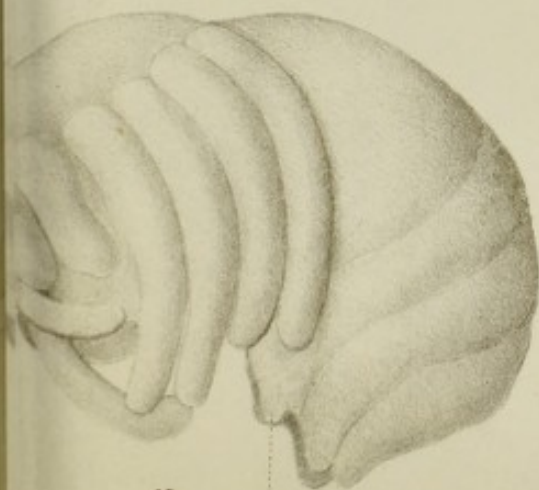
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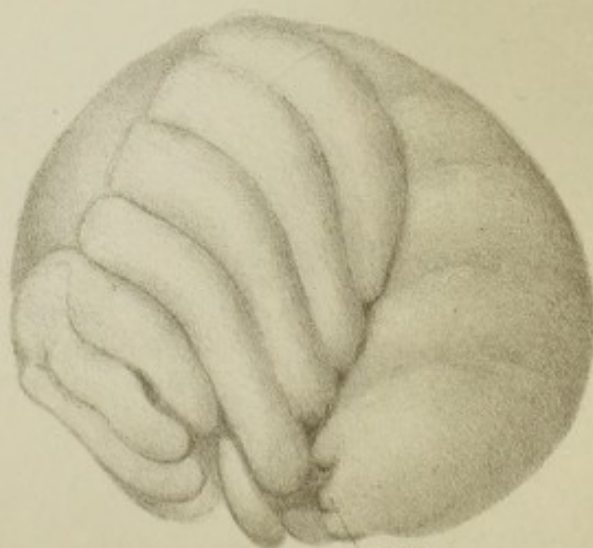
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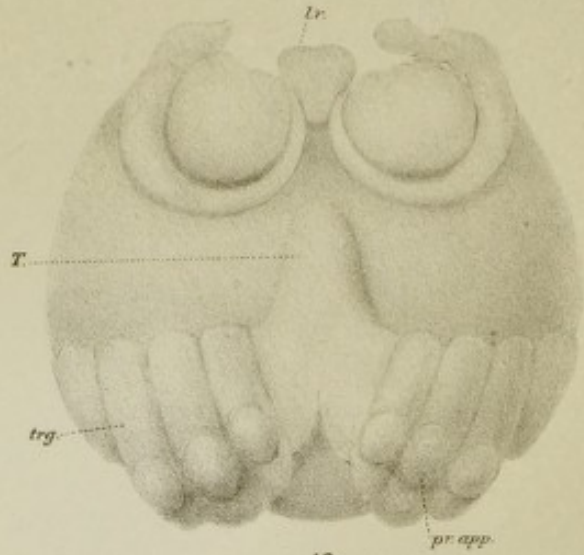




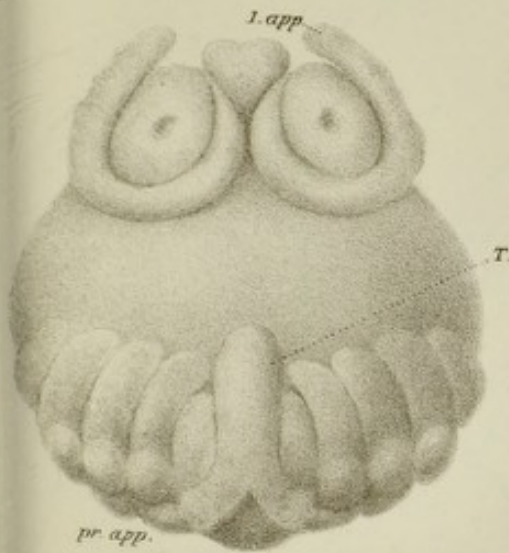




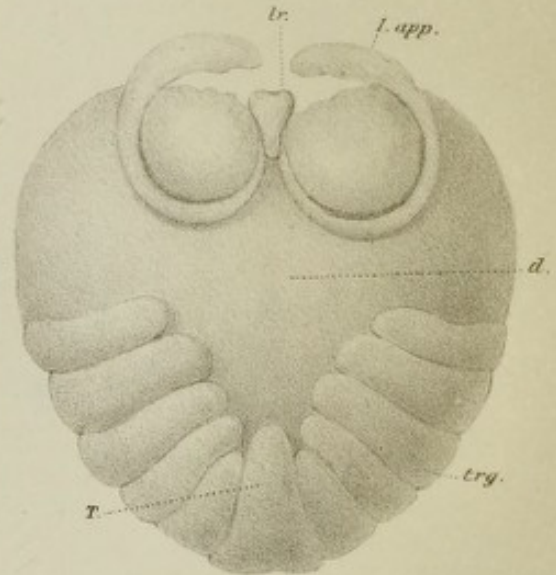
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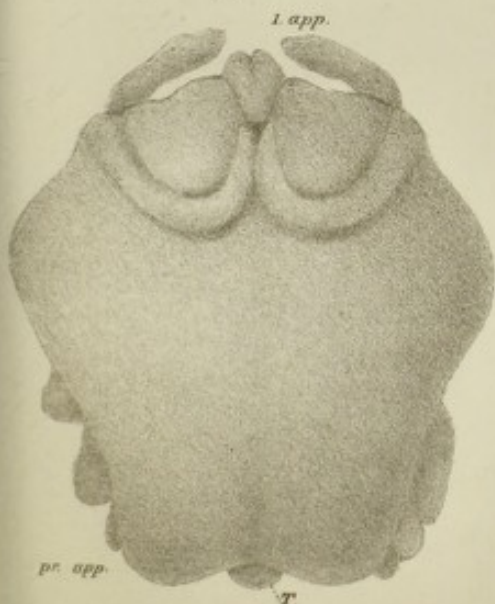
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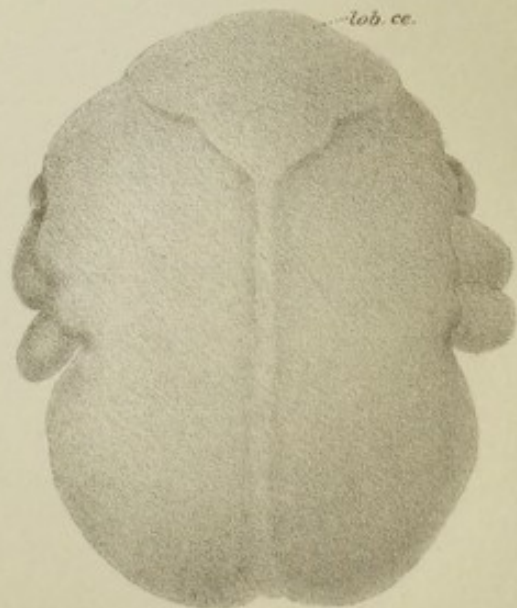
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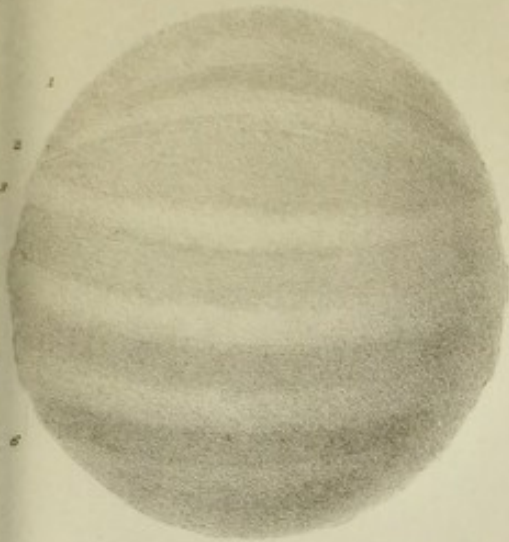
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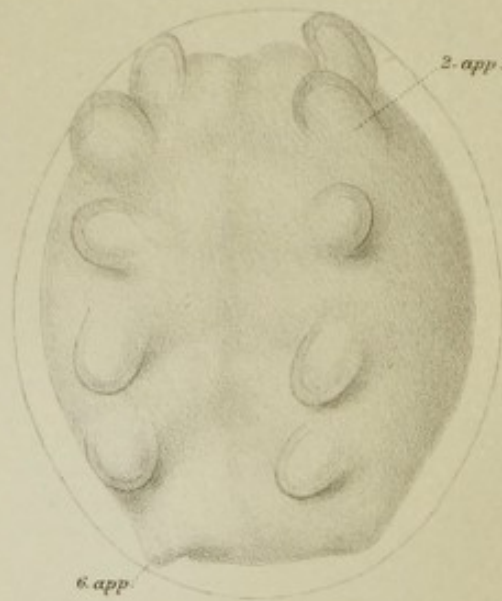
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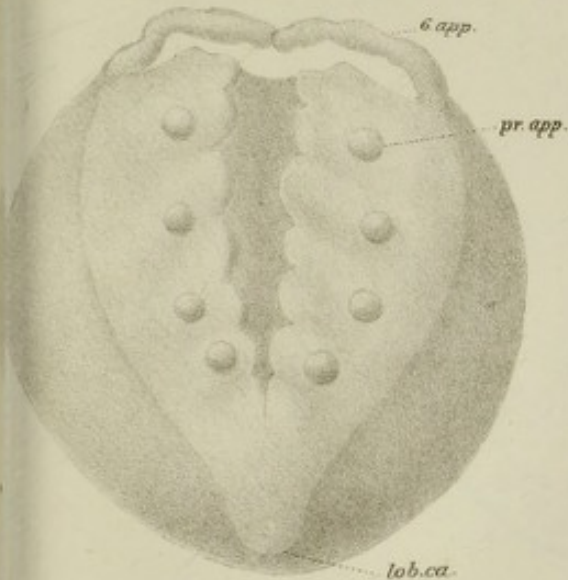




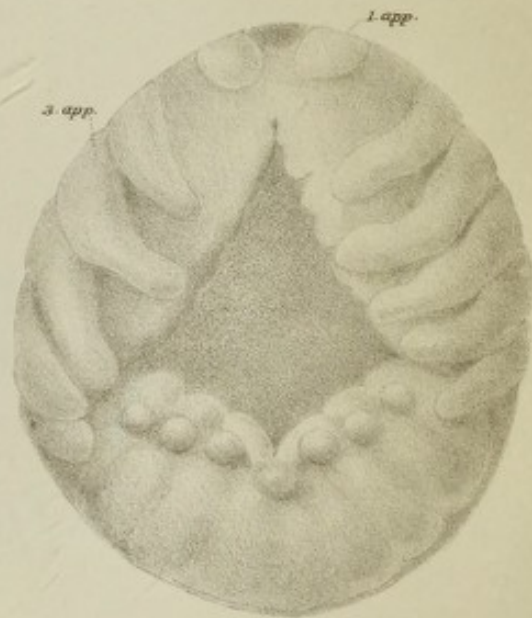
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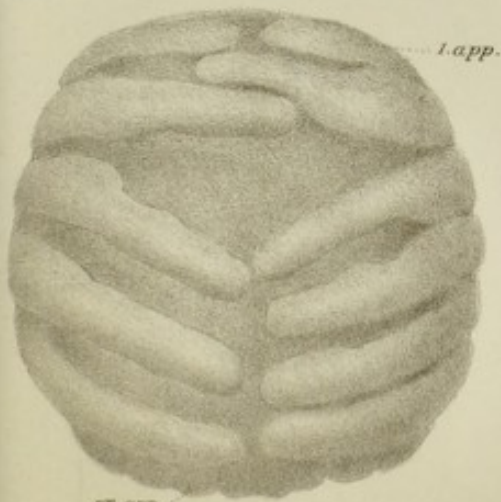
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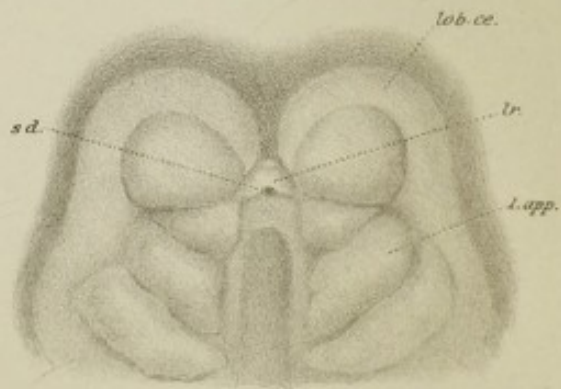
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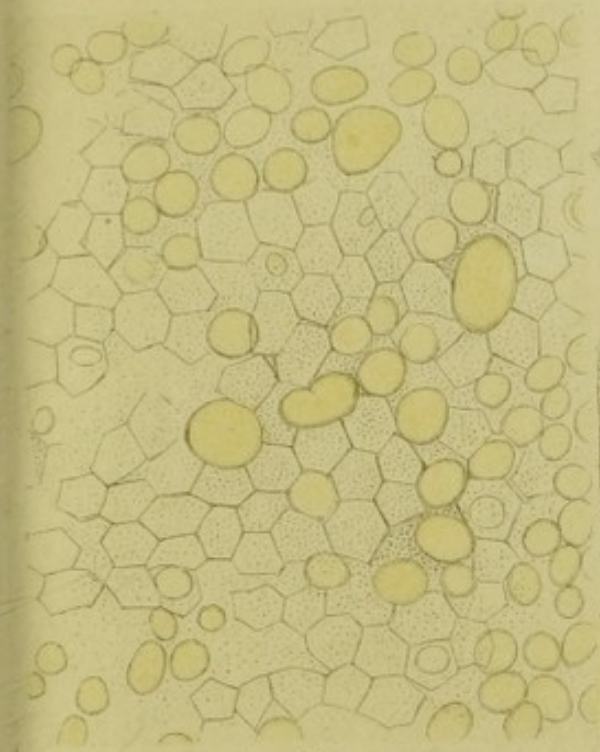
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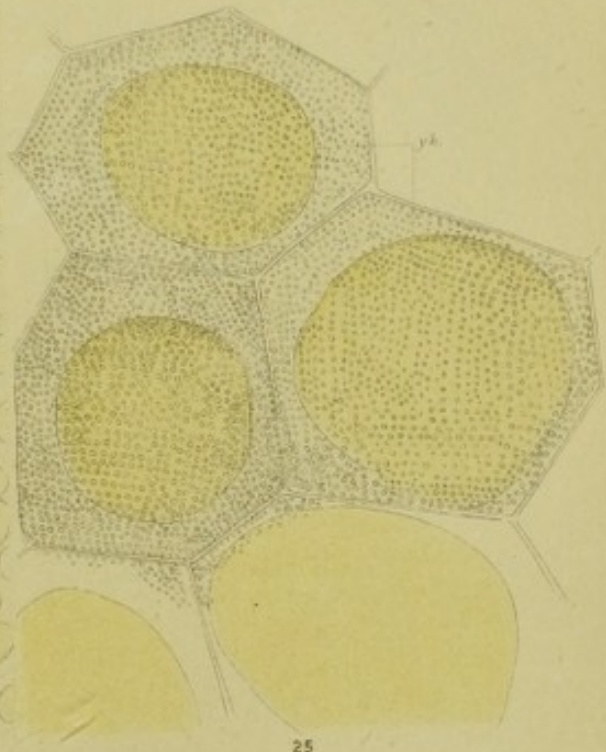
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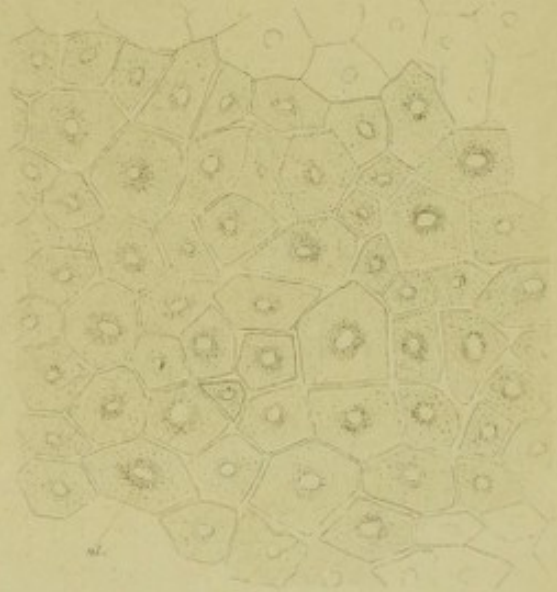
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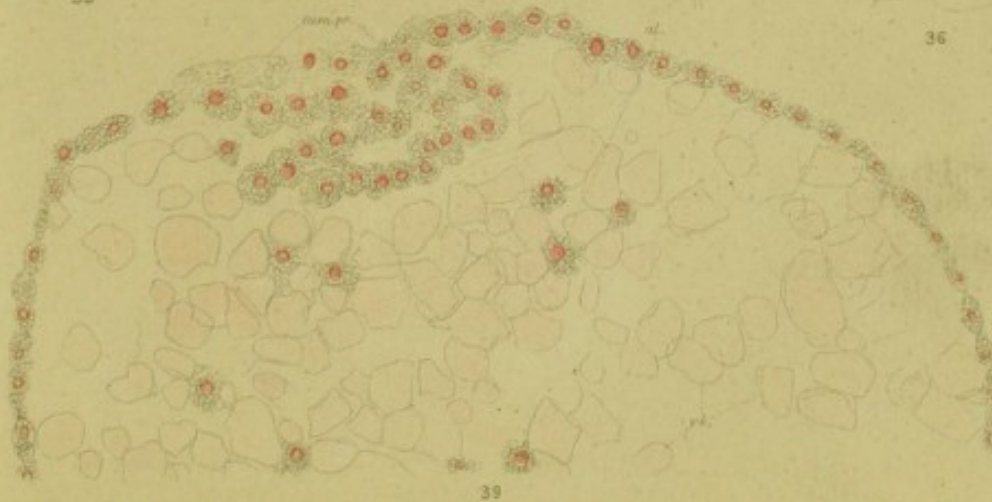
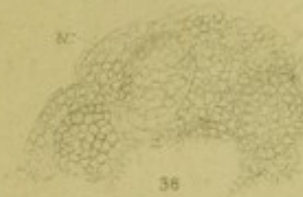
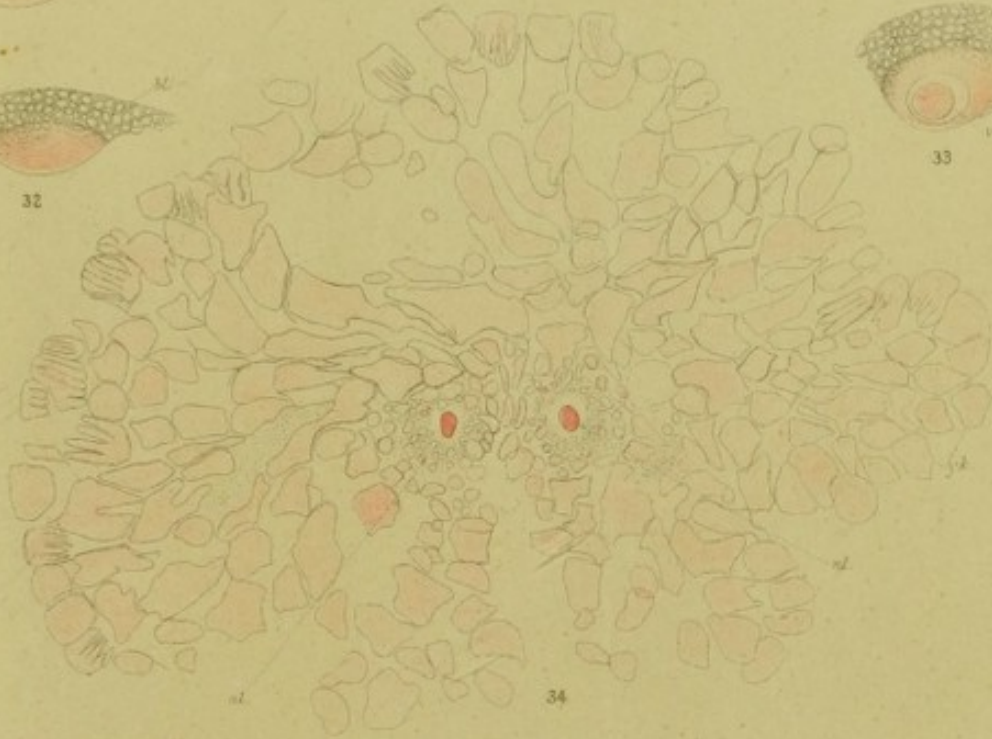
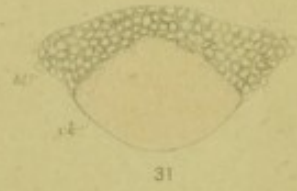
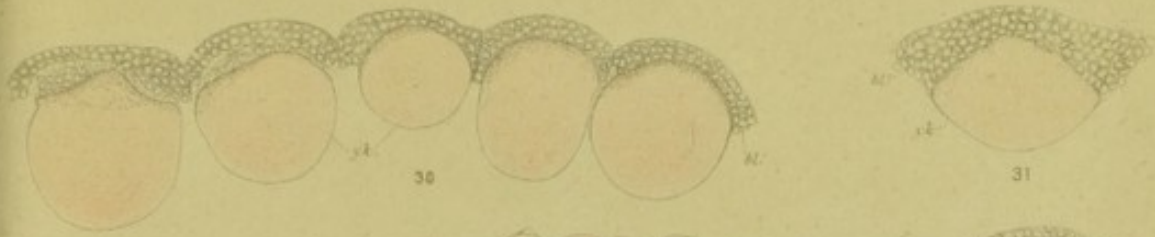
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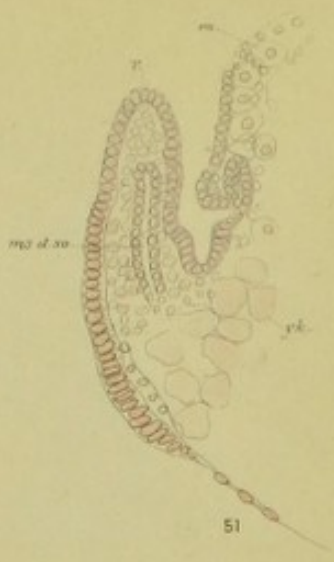








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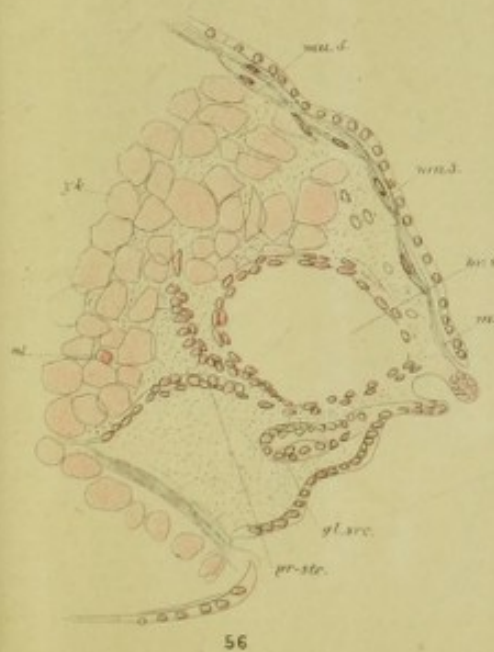
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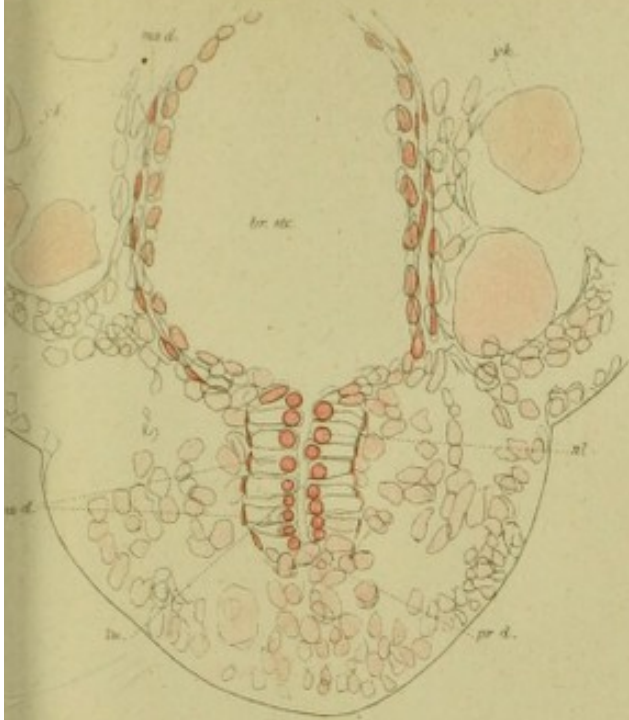
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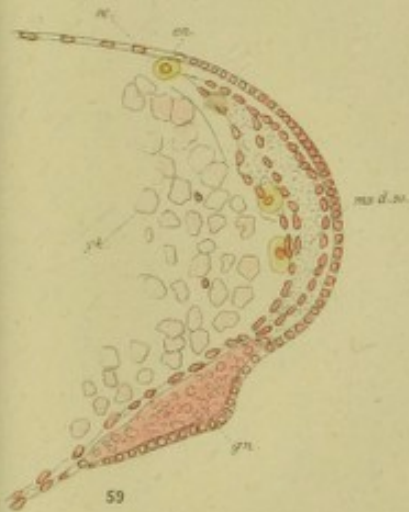




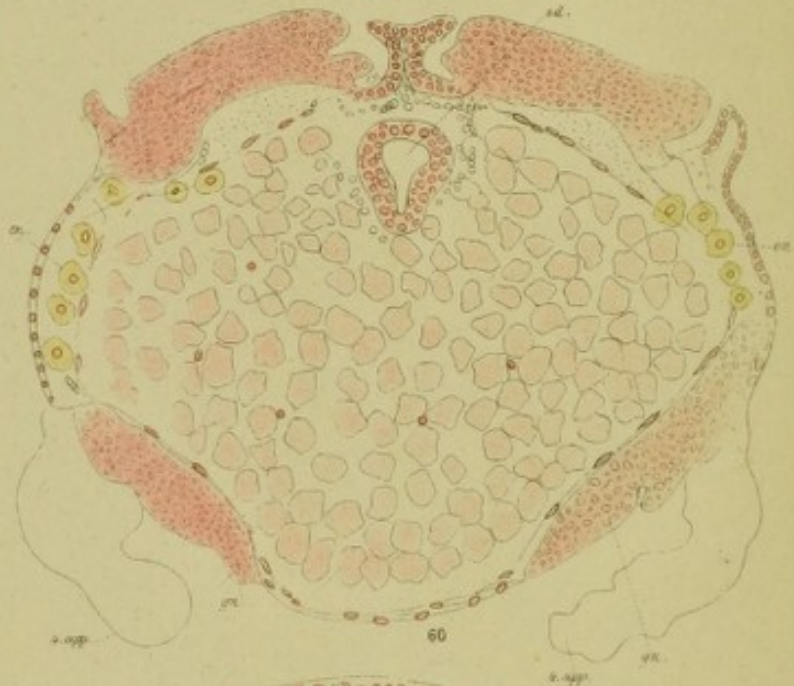
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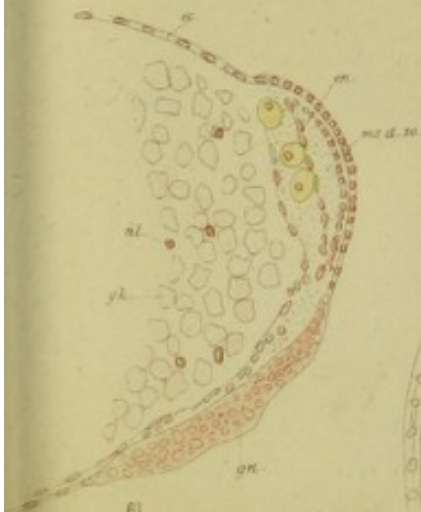
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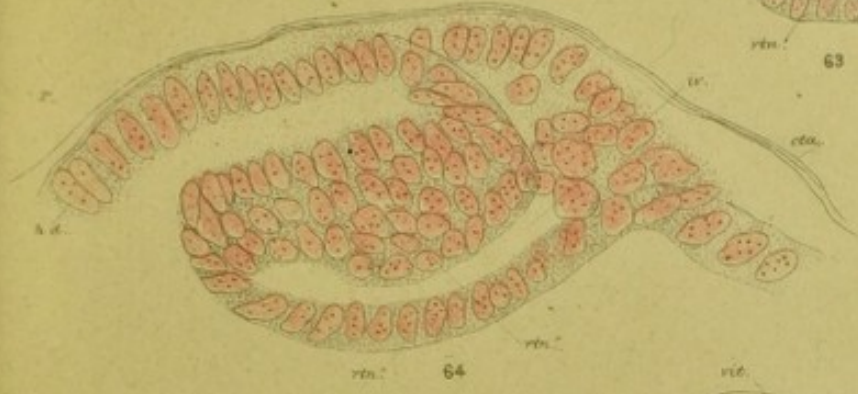
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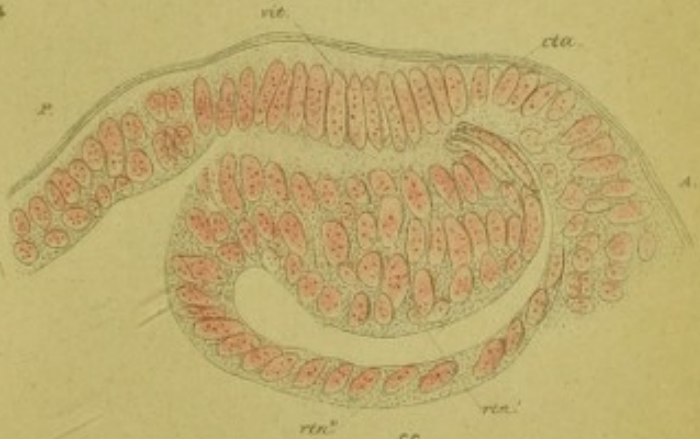




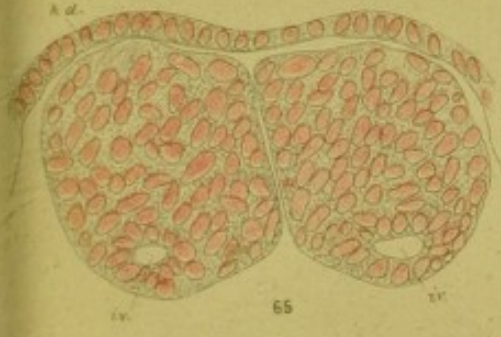
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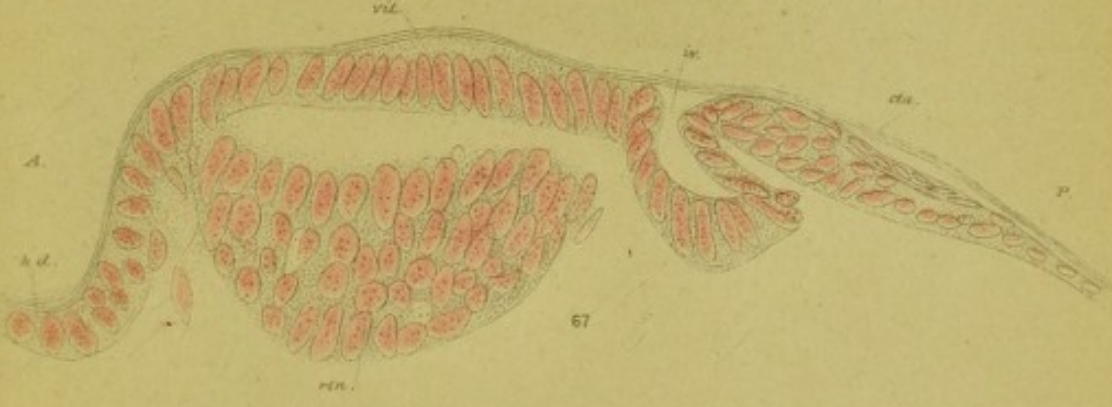
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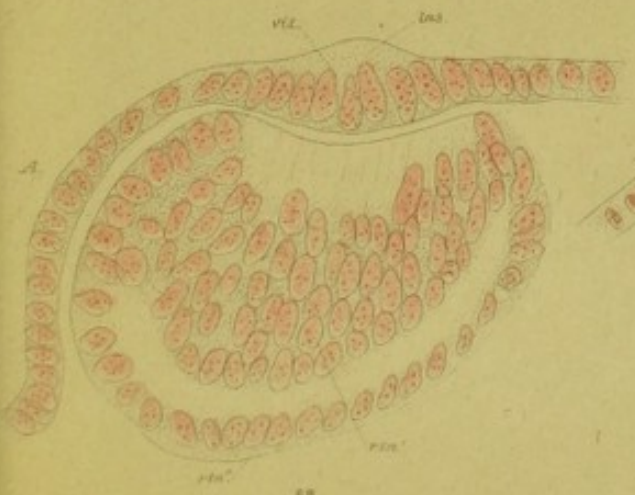
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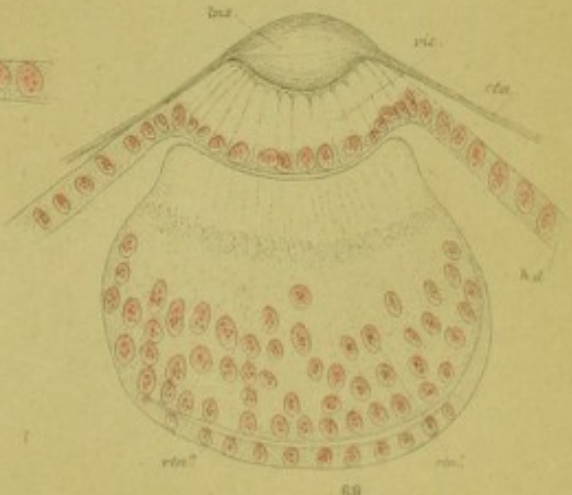
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