

### III.

#### *Embryology of the Ctenophoræ.*

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DURING the summers, from 1860 to 1863, I succeeded in tracing the growth of several of the species of Ctenophoræ common on the shores of New England. The stages to which my attention was principally given were those succeeding the escape from the egg. The most interesting of them were figured as woodcuts in my North American Acalephæ, in 1865. At that time some attention was also paid to the earlier conditions of the egg and the principal phases were observed, but the observations were too incomplete for publication. Enough, however, was seen to show a most extraordinary mode of segmentation, the more important of these phases have since been traced by Kowalevsky and partially confirmed by the observations of Fol. The changes of the embryo showed, as had already been suggested by Müller and Gegenbaur, no trace of a metamorphosis. It is a direct development from the egg to the adult.

I have, during the past summer, filled the blanks in my observations and am now able to give a connected account of the history of one of our species (*Idyia roseola*) from the earliest stages in the egg until it has all the features of the adult; also a somewhat less complete embryology of a second species (*Pleurobrachia rhododactyla*<sup>1</sup>) as well as fragments of the development of several other genera. This, taken in connection with what has been published regarding the development of other Ctenophoræ, gives us a tolerable view of the mode of development of the order, concerning which so little was known until quite recently.

<sup>1</sup>The question of the identity of these two species with the European *Beroë ovata* and *Cydippe pileus* must probably be answered in the affirmative. The number of species now recognized as common to both sides of the Atlantic is so great that, from want of positive evidence to the contrary, it will be most natural to consider them as identical. Many of the species of Ctenophoræ are now known to have a wide geographical range on the European shores from the North Atlantic to the Mediterranean, and on our shores the same species (?) of Pleurobrachia and Idyia probably occur on the Atlantic and on the Pacific sides of North America.

In the oldest observations on the development of *Ctenophoræ* by Price,<sup>2</sup> he already noticed the early agreement in structure between the young *Beroë* and the adult, and describes quite accurately the general mode of the growth of *Cydidippe* within the egg. Price was specially struck with the fantastic movements of the young *Cydidippe* within the egg envelope, its "nursery."

Allman<sup>3</sup> noticed the simple nature of the edge of the tentacular disk; he further described the difference in the mode of segmentation of some of the masses; he regards them, however, as different stages in the process of segmentation; he has called attention to the composition of the egg as made up of two portions, a central one composed of large spherical cells, and a peripheral one of much smaller cells. He has also given quite in detail the general course of the changes undergone by *Beroë*, but unfortunately, as the descriptions are not accompanied by figures, the paper of Allman has not received the attention it deserves, and neither Kowalevsky nor myself,<sup>4</sup> who have followed him, gave him the credit for the completeness of his observations, apparent in every line of his carefully worded note, which, as far as *Beroë* is concerned, gives us an excellent summary of its embryonic history.

Kowalevsky's<sup>5</sup> Memoir, written some time after my own observations, was mainly devoted to the early stages of the egg, and being accompanied by good figures has placed the embryology of the *Ctenophoræ* on a basis to be understood by all who have not had the opportunity to follow their development for themselves, and to whom Allman's paper would be unintelligible. Fol's<sup>6</sup> observations fully corroborated the principal novel points observed by Kowalevsky, and in the Memoir here published I have given a more connected history of two species than could be brought together from the papers of my predecessors. Before Kowalevsky and Fol, Gegenbaur,<sup>7</sup> Semper,<sup>8</sup> Claus<sup>9</sup> and M'Crady<sup>10</sup> had given attention to special points; Semper to the peculiar mode of segmentation of *Ctenophoræ*;

<sup>2</sup>PRICE, JOHN. Embryogeny of Ciliogrades. Proc. Brit. Assoc. Adv. Sci., 1846, Trans. Sect. p. 87 (1847).

<sup>3</sup>ALLMAN, GEO. J. Contributions to our Knowledge of the Structure and Development of the Beroïdæ. Proc. R. S., Edinbg., Jan., 1862, iv, p. 519. Same, Edinbg. Phil. Journ., 1862, xv, p. 284.

<sup>4</sup>AGASSIZ, ALEXANDER. North American Acalephæ. Ill. Cat. M. C. Z., No. II, 1865; see also AGASSIZ, ELIZABETH C. and ALEXANDER, Seaside Studies, 1863.

<sup>5</sup>KOWALEVSKY, A. Entwicklungsgeschichte der Rippenquallen. Mém. Acad. St. Pétersb., x, No. 4.

<sup>6</sup>FOL, H. Ein Beitrag z. Anat. u. Entwickel. einiger Rippenquallen, 1869.

<sup>7</sup>GEGENBAUR, K. Studien ueber Organisation u. Systematik der Ctenophoren. Archiv. f. Naturg., xxii, 1856.

<sup>8</sup>SEMPER, C. Entwicklung der Eucharis multicornis. Zeit. f. Wiss. Zool. 1858.

<sup>9</sup>CLAUS, C. Bemerkungen ueber Ctenophoren u. Medusen. Zeit. f. Wiss. Zool. xiv, 1864.

<sup>10</sup>M'CRADY, JOHN. Development of two species of *Ctenophoræ*. Proc. Elliott Soc. Nat. Hist. 1857.

Gegenbaur, Wagener, Claus and others figured a few of the young stages after their escape from the egg, while to M'Crady we owe the important observation that the younger stages of *Bolina* differ widely from the adult, thus supplementing the notice of the direct development of Ctenophoræ by Müller, Boeck and Wright by showing, that although Ctenophoræ were undoubtedly reproduced from eggs, and at an early age gave unmistakable signs of their parentage, yet, that the changes of form the young undergo before they assume the aspect of the parent are very great in some families.

The greater part of the materials I obtained in former years was fished up at night with the hand net. A small part was also obtained in the morning and late in the afternoon during perfectly smooth weather. By keeping the adult alive I managed to raise the young from the eggs laid in confinement, and was thus able to keep a constant supply of the different stages on hand. Ctenophoræ are readily kept in confinement, and after a lapse of from twelve to twenty-four hours after they are captured they usually lay eggs. These were then picked out and placed in separate jars, and by simply changing the water, three to four times daily, the majority of the eggs developed successfully.

All Ctenophoræ come to the surface of the water whenever it is smooth, at all times of the day; they are found in the greatest number between the hours of nine and eleven in the morning, and from four to six in the afternoon, in the summer and fall. Sometimes *Pleurobrachia* is very common near the surface even in rough weather, but *Idyia* and *Bolina* always move below the surface, the deeper the more the water is disturbed. Although the Ctenophoræ are hermaphrodites, yet when they come to the surface and associate as they do in large patches, they probably come to spawn, as the water round them is filled with eggs floating a few inches below the surface, until the impurities in the water are collected upon the envelope in sufficient quantity to cause them to sink. It is important to remove the eggs of *Bolina* and *Idyia* from the jars in which they have been laid, on account of the great mass of slime emitted by the adult medusæ, which renders the water foul. The eggs of *Pleurobrachia* escape singly. Kowalevsky says the eggs are laid in strings. I have only seen this in the case of the eggs of *Bolina*, in which the eggs are laid in strings of from ten to twelve; the eggs of *Idyia* are laid embedded in a thick, slimy mass. Our Ctenophoræ spawn late in the summer and fall, during the last part of July, August and September, while according to Kowalevsky some of the Ctenophoræ found in the Mediterranean lay their eggs during the whole year, and individuals of different sizes are con-

stantly found together. On our shores they spawn only during a very limited period, as stated above; the young brood, developed during the fall, comes to the surface again the following spring as nearly full grown Ctenophoræ, to lay their eggs late in the summer. The Idyias appear to attain their full size quite early, while Bolina and Pleurobrachia I have not met of large size till later in the summer or fall. The autumn brood most probably passes the whole winter in deep water, and it must take six to eight months for the young Ctenophore to attain its maturity. All the young Ctenophoræ I have had alive passed the greater part of the time at the bottom of the vessels in which they were kept.

The genera found south of Cape Cod, in Buzzard's Bay and Narragansett Bay, attained their maturity much earlier, and appear full grown in the waters along the southern coast of New England as early as May. I have had eggs of Lesueuria and of Mnemiopsis in May, June and July. All the Ctenophoræ are more brilliantly colored at the time of spawning. Idyia is naturally more brilliant than the other genera, the whole of the gelatinous tissue being of a marked pink color, while in Bolina and Mnemiopsis it is of a delicate steel color, or nearly transparent and colorless; in Mertensia it is brilliant carmine, while Pleurobrachia is more or less yellowish with an orange or carmine tint; after they have spawned they are entirely colorless. The most brilliant coloring patches are limited to the genital organs, the spermaries being readily distinguished in Idyia and Pleurobrachia by their more vivid color. In Idyia the genital organs are placed on the sides of the main chymiferous tubes; they form branches extending far into the body of the gelatinous tissue; on one side of the main tube are the spermaries, on the other the ovaries. Their arrangement has been well described by Will, and also by Agassiz. The genital organs of Pleurobrachia are somewhat differently situated; the spermaries (Pl. V, fig. 31; 32, *s*) and ovaries (Pl. V, fig. 31; 32, *e*) are in the main chymiferous tube itself (Pl. V, fig. 31; 32, *ch*), extending towards the actinal extremity on the inner side of the main chymiferous tubes which, as is well known, do not branch; a similar disposition of the genital organs has also been figured by Fol in Vexillaria (Cestum).

In all the eggs of Ctenophoræ I have studied, their great transparency renders it easy to follow the early stages of the segmentation and the growth of the embryo; in Idyia, up to the time when pigment spots are developed, in Pleurobrachia and Bolina the transparency of the embryo is retained not only till it leaves the egg envelope but also while the embryo passes through many of its subsequent stages.

I shall describe in detail the successive phases of development in *Idyia*, and only refer in the other genera to the corresponding stages of growth, which will be fully explained in the descriptions of the Plates. The earlier stages in the egg do not differ materially in the different genera; it is only when the family features begin to appear in the embryo, that we find a marked difference in the subsequent development of the representatives of the simple and of the tentacle bearing families.

## IDYIA ROSEOLA.

*Idyia roseola* AGASS. Cont. N. H. U. S. III, 1860.

EGGS OF IDYIA.—The eggs of *Idyia* are about 0.5<sup>mm</sup> to 0.6<sup>mm</sup> in diameter, the ratio of the diameter of the outer envelope to that of the yolk mass, being 1.3:1. [The eggs of *Pleurobrachia* are considerably larger, from 0.85<sup>mm</sup> to 1.00<sup>mm</sup> in diameter, and the ratio of the diameter of the outer envelope to the yolk is 3.5 to 1.] The outer envelope is perfectly transparent, without apparent structure; it surrounds a yolk mass filling a comparatively large portion of the space of the interior (Pl. I, fig. 1). This seems to be a characteristic feature of the eggs of the *Beroidæ* in contrast with those of the *Cydippidæ*, in which the yolk mass is proportionately much smaller although the eggs themselves are larger (Pl. IV, fig. 1); the yolk mass of the eggs of the *Beroidæ* is less transparent than in the *Cydippidæ* and *Bolinidæ*, as has been also noticed by Kowalevsky. The space between the outer envelope and the yolk mass is probably filled with seawater; there seemed no distinction between the inner, clear, transparent fluid and the surrounding salt-water. This is rendered very probable from the fact that the young *Pleurobrachia*, which remains in the egg envelope a comparatively longer time than *Idyia*, goes through (within the envelope) all the evolutions which it performs in the open sea after its escape from the egg. The yolk mass of the eggs of *Idyia* (and all *Ctenophoræ*) consists (after they are laid) of two layers, an inner yolk mass more or less fatty (Pl. I, fig. 2) made up of large, irregular spheres. This inner yolk mass is surrounded by a second thin, outer layer, finely granular. This outer layer and its enclosed central mass perform very different parts in the development of the embryo, and it is of the utmost importance to keep the changes these two layers undergo, clearly distinct, while following the development of the young *Ctenophore*. The outer layer, as has been shown by Kowalevsky, is eminently the embryonic layer, while the inner mass acts as a mere nutritive yolk mass. Traces of this yolk mass are still very apparent in some of the oldest stages raised from the egg, both in *Pleurobrachia* and in *Idyia*. I have already described a similar yolk mass while tracing the growth of the early stages of *Arachnactis*<sup>11</sup> (*Edwardsia*) and have shown that it is at the expense of this yolk mass that the changes going on in the interior of

<sup>11</sup>AGASSIZ, A. *Arachnactis brachiolata*. Proc. Bost. Soc. N. H., 1863, p. 525.

the young *Actinia* take place, much as we shall describe them in the growth of the inner organs of the *Ctenophoræ*.

FIRST TRACE OF SEGMENTATION.—I have noticed the same movements of the outer layer of the yolk, observed by Kowalevsky, which press the inner yolk mass either to one side or the other (Pl. I, fig. 2, *c'*, ) by the contractions of the outer layer, so that the yolk mass loses its regular, circular outline, becoming gibbous on one side or the other. These movements appear to be the first sign of the segmentations of the yolk. I have never succeeded in seeing a germinative vesicle or nucleus in any of the eggs of *Ctenophoræ*, after they were once laid. By the motion of the outer layer a thickening is thus formed at one side (Pl. I, fig. 3) producing two slight protuberances, *c' c'* which go on increasing in size (Pl. I, fig. 4) until they form a small furrow between them. This furrow penetrates deeper and deeper (Pl. I, fig. 5) into the mass of the yolk (Pl. I, fig. 6); at the same time the two prominences first formed gradually approach and eventually are placed in contact (Pl. I, fig. 7). The outer layer during this segmentation gradually encroaches upon the surface of the two spheres formed (Pl. I, fig. 7), and by the time the segmentation into two is nearly complete, the spheres are connected by a mere bridge (Pl. I, fig. 8); this bridge, however, also disappears, and at last we have two independent spheres, each consisting of the same two layers so characteristic of the original yolk mass (Pl. I, fig. 9). The first segmentation into two just described is now repeated by exactly the same process for each of the two spheres. There is a thickening of the outer layer, a depression is formed at right angles to the first segmentation (Pl. I, fig. 10), this little by little grows deeper and deeper (Pl. I, figs. 11, 16) till at last we have four spheres still connected by bridges (Pl. I, figs. 12–18). The only difference between the first segmentation and the subsequent subdivisions of the yolk appears to be in the absence of the movements of the outer yolk layer characterizing the appearance of the first segmentations. The different figures of each stage (Pl. I) will be better than any description I can give of the shape of the spheres<sup>12</sup> in the successive phases of development. The bridge is always placed on the side opposite to which the segmentation commences; Pl. I, figs. 14, 15 are views of the same stage from opposite poles. Up to this stage there is no difference in the size of the spheres, they are all equal, but in the subsequent

<sup>12</sup> I use the word sphere merely to denote the components of a segmented mass.

stages (Pl. I, figs. 17–25) we have a marked difference in the size of the new spheres of segmentation. The four spheres of segmentation have, like the original yolk mass (Pl. I, fig. 8), an outer layer and an inner mass. The outer layer is somewhat thickened on the exterior sides at points, which, when the segmentation commences, will divide the original sphere obliquely into two spheres of very unequal size (Pl. I, fig. 17); but the mode of segmentation is absolutely the same and the result reached is also identical, viz: eight spheres of segmentation (of different sizes), each consisting of a thin outer embryonic layer and an inner yolk mass of fatty spheres.

SECOND STAGE OF SEGMENTATION.—The stage just reached is an important one, as the subsequent segmentation takes place mainly at specified points. On examining the various figures given of this stage (Pl. I, figs. 17–25) we observe that the spheres arrange themselves round a vertical axis, and that at the same time a longitudinal axis is formed. In the vertical axis we easily distinguish two opposite poles (Pl. I, fig. 24) while the extremities of the longitudinal axis are similar. This is emphatically the stage in which the embryo begins to form; the segmentation henceforth, though similar in all its essential features to that previously described, is limited to one pole of the spheres; to the pole which eventually corresponds to the actinostome of the adult. Small spheres of segmentation are formed, materially different from the larger yolk spheres; the layer thus indicated at the actinal pole gradually covers the whole of the surface of the yolk spheres, forming a complete outer envelope; from this outer envelope the external organs of the *Ctenophoræ* are built, while, as we shall see hereafter, the large inner spheres form a yolk mass, at the expense of which the internal organs and the body walls of the young are developed.

FORMATION OF THE EMBRYONAL LAYER.—There is, in the stages of the yolk thus far described, no trace whatever of a nucleus; the whole tendency to segmentation appears to come from the outer finely granular layer. As is shown in Pl. I, fig. 26, the mass of the outer layer accumulates at the small end of the spheres, and there begins a most active segmentation, limited, however, to a portion only of the actinal part of each sphere. This is most readily seen in the next stages, Pl. I, figs. 28–30, showing the mode of formation of the ring of small spheres at the pointed extremity of the larger spheres. It is from these small spheres formed by segmentation of a part of the sphere, in exactly the same



manner as the original segmentation of the primary yolk, that the true embryonic layer is formed. So that henceforth we have an independent segmentation of the eight small spheres, formed from the actinal part of the eight large spheres, the bulk of which, the abactinal part, remains to form the nutritive yolk of the future embryo. The inner mass seems, as far as I have been able to observe it in the early stages of the segmentation, to follow passively the rapid segmentation going on to form the outer layer. The eight small actinal spheres segment in the same manner as the larger spheres, the spheres all passing through a sort of dumb-bell shape, so characteristic of the earlier stages (as in Pl. I, figs. 16, 17, 29, 31, 33). A very well defined nucleus appears at about this stage, in the small darker spheres of the actinal pole (Pl. I, fig. 36). I have not succeeded any better than Kowalevsky in tracing the origin of this nucleus. The segmentation of the actinal portion of the small spheres takes place very rapidly, while during the same time no change whatever takes place in the eight large spheres (Pl. I, figs. 35-39); they are merely compressed closely together, the small spheres forming a ring, as it were, soldered upon the actinal part of the large spheres. There is an actinal depression formed surrounded by the smaller spheres; between the larger spheres, along their vertical line of contact, an elliptical cavity more or less compressed runs through the axis of the embryo (Pl. I, fig. 30). From the nucleus of the small spheres irregularly branching lines extend to their periphery.

SEGMENTATION OF THE LARGE SPHERES.—As has been observed by Kowalevsky the large spheres in some genera go through a slower segmentation, but as far as I have observed it in *Idyia*, *Bolina* and *Pleurobrachia* beyond the number of eight spheres, the segmentation is quite irregular. In Pl. I, fig. 40, we have the large spheres again divided into eight; additional spheres quite irregular in size were placed at the actinal pole of the embryo, Pl. I, fig. 43; the small actinal spheres of the elliptical ring are now closely packed together; they commence to spread over the surface of the large spheres, extending gradually (Pl. II, fig. 7) so as to cover the whole of the embryo.

In the last stages described, after the brisk segmentation of the small spheres commences, it is no longer possible to distinguish as readily as before the precise limits of the large spheres. The two axes, the vertical and the longitudinal which are so early developed by the peculiar arrangement of the spheres, become better marked owing to the lateral flattening of the embryo (Pl. I, fig. 42). The walls of the embryo, over the large spheres, have become much thickened (Pl. I, fig. 44),

especially near the actinal pole where the most rapid increase of the small cells of the embryonic layer is to take place (Pl. I, fig. 45); these small spheres diminish gradually toward the opposite pole, and in a view seen from that end show quite a large part of the sixteen primary spheres as yet not covered by them (Pl. I, fig. 46). There is still quite a deep elliptical trench left at the actinal pole, into which the smaller spheres are gradually pushing their way down; as is seen in Pl. II, figs. 1, 2, the small spheres arise in irregular patches, often disconnected, on the surface of the large yolk spheres near the actinal pole; in Pl. II, fig. 5, we have an indistinct mulberry stage, as it were, over the whole actinal part of the embryo; this does not yet extend over the opposite part of the embryo, Pl. II, fig. 3. In Pl. II, fig. 7, the whole embryo, with the exception of a small circular portion of the abactinal region, is completely covered by the embryonic layer of small spheres; in the next stage, Pl. II, fig. 12, this space is nearly closed; it is completely closed in Pl. II, fig. 8.

FORMATION OF THE OUTER WALL.—While the small spheres thus extend towards the abactinal pole over the large yolk spheres, they are always most prominent at the actinal pole. When seen in profile we obtain interesting views of the structure of the embryo (Pl. II, figs. 9, 10); the outline has become quite cup-shaped, the small spheres are most prominently developed round the actinostome (Pl. II, fig. 11), while at the same time the irregular outlines of the original large yolk spheres can still be easily traced. The outline seen in profile is now somewhat depressed at both poles (Pl. II, fig. 13) and through the outer wall, composed of small spheres covering the whole of the inner yolk mass, we can trace the indistinct outlines of the large yolk cells closely packed together; through the axis of the embryo their lines of contact form an apparent elliptical cavity. The small spheres have become quite minute, and have so encroached upon the actinal surface as to close the whole of the cavity formerly existing, which has been entirely obliterated by the close contact of the small spheres of the actinal surface. The embryo in this stage consists of an outer envelope made up of small spheres (the outer germinal layer), all having a central nucleus with a granular structure; this outer envelope is somewhat thicker at the actinal pole; through it the outline of the central yolk mass, consisting of large irregularly limited spheres, can be traced.

FORMATION OF THE ACTINOSTOME.—The outer walls having thus been formed

by the gradual encroachment of the actinal cells over the whole of the yolk mass till we reach the condition of the embryo of Pl. II, fig. 13, the next stages consist in the thickening of the outer walls at special points (Pl. II, fig. 14, *v, a*). We find near the abactinal pole a marked increase in the spheres, the first trace of the locomotive flappers, *v, v*, and at the same time a great increase in the number of the spheres of the embryonic layer at the actinostome, *a*, accompanied by a slight depression. In the following stages the accumulations of the spheres to form the locomotive flappers are still better marked (Pl. II, figs. 15, 16). At the same time we find the first trace of a rudimentary swelling at the abactinal pole, which is to form the sensitive bulb. It will be noticed that in several of the figures, not only of this stage but also of others, the same point of development is not always reached equally for all the parts; it quite frequently happens, as here for instance, that the spheres of the locomotive flappers are more advanced in proportion to the development of the actinostome, which is further advanced in a preceding stage. The inner yolk mass appears, as far as can be judged from an exterior view, to break up into irregularly shaped spheres, pressed together closely, the indistinct outlines of which appear through the outer wall; though in stages much further advanced in other respects, we often can, in a profile view, see indistinctly the outlines of the original sixteen large spheres more or less broken up into partial spheres (Pl. II, fig. 17).

FORMATION OF THE DIGESTIVE CAVITY.—(Pl. II, fig. 17.) In this stage the cells of the embryonic layer have pushed their way towards the abactinal pole, the digestive cavity appearing at present as a mere conical opening extending but little ways from the actinostome proper. This, when seen from the actinal side, already has the appearance of a well defined opening. As fast as the digestive cavity increases in length (Pl. II, figs. 19, 20) the walls become thicker and better defined, gradually approaching (Pl. II, fig. 25) till the upper extremity of the cavity touches the walls of the abactinal part of the embryo. The mode in which the cells force their way upward from the actinostome between the large yolk spheres, on their surface, is best seen in Pl. II, fig. 21, in which the actinostome is quite retarded, considering the great development of the otolite and of the locomotive flappers. A clear space often appears to be formed at the abactinal extremity of the digestive cavity into which it seems to open; it is only the interstitial space between the large yolk masses formed by the contraction, as it were, of the yolk masses, forming very thick walls round the remaining more trans-

parent yolk mass. The first trace of these walls is seen in Pl. II, fig. 22, while the contrast between the more segmented and clear inner yolk mass is quite well shown in Pl. II, figs. 26, 27.

**THE YOLK MASS AND ITS FUNCTIONS.**—The function of the yolk mass, as the basis of the internal organs of Ctenophoræ is best shown by the few stages immediately following those just described. At the time when we have the first trace formed of the gelatinous tissue, or the tissue of the principal mass of Ctenophoræ, the relation to the outer walls, and difference existing between the inner transparent parts of the yolk mass, are well shown in any of the views from above of the embryos at this stage (Pl. II, figs. 30–32); while in the profile view we see the first trace of the connective tissue formed at the base of the actinostome (Pl. II, figs. 29; 25, *t*; 23, *t*). The passage of the cells of the yolk mass into the connecting tissue is a very remarkable phenomenon, and explains most satisfactorily the structure of the Ctenophoræ, regarding which so many contradictory views were held up to the present time. The view of Agassiz must yield to that first proposed by Kölliker and now fully demonstrated by Kowalevsky, Fol and myself, that the long thread-like nuclei are not the dividing lines of the cells of the tissue, but are elongated cells encased within the mass forming the connecting tissue, which have passed from the yolk mass directly into the tissue.

By examining a young embryo at the stage of Pl. II, fig. 33, somewhat inclined, we can easily see the accumulation of cells upon the surface of the yolk mass at the point where the most active action is going on, and where the connecting tissue is forming between the two inner yolk masses and the outer wall. Seen from above we should have very much the same view as in Pl. II, fig. 39, only the walls of cells enclosing the yolk mass would appear much thinner (Pl. II, fig. 32). The gradual increase in size of the central transparent yolk mass, as fast as the connecting tissue is formed at the expense of the outer part of the yolk mass is clearly shown in Pl. II, figs. 34–40, Pl. III, figs. 1–9, the space occupied by the connecting tissue becomes thicker and thicker until at last the yolk mass is reduced to mere walls enclosing a central clear yolk mass, having all the appearances of a tube and readily mistaken for one (Pl. III, figs. 6; 9, *y*). It is not till later that the lateral tubes make their appearance, forcing their way down from the original digestive cavity toward the actinostome. The connecting tissue is also rapidly developed adjoining the digestive cavity (Pl. III, figs. 2–4),

so that the remaining portions of the yolk mass project through the middle of the mass, half-way from the cavity to the outer wall.

**CHYMIFEROUS TUBES.**—By the time the connecting tissue forms the whole of the actinal portion of the young Ctenophore, the digestive cavity proper, at first a small elliptical opening (Pl. II, fig. 33), which has gradually been increasing in size (Pl. II, fig. 38, Pl. III, fig. 3), commences to bulge out laterally, throwing out four pouches, which push their way rapidly outward and towards the actinal pole. The portions of the yolk mass remaining in the abactinal part of the embryo, clustering round these pouches, form, as it were, thick walls at the expense of which these pouches are first formed (Pl. III, figs. 7–9); the connecting tissue develops quite rapidly at the abactinal pole, and isolates the upper part of the chymiferous tubes (forming the short funnel) from the abactinal walls of the embryo. There remains in this stage nothing of the yolk mass except a short triangular mass into which the base of the lateral tube soon pushes its way.

**LOCOMOTIVE FLAPPERS.**—The locomotive flappers are at first, short, stiff, immovable points (Pl. II, fig. 19), mere prolongations of the cells of the outer layer, accumulated along the line where the flappers are to appear. These flappers as they increase in length become more and more movable (Pl. II, figs. 21, 26), till at last they form in the young *Idyia* (Pl. II, fig. 37, Pl. III, fig. 9) rows of quite long flappers in incessant motion. Their composition has already been well described by Grant, Agassiz and others. Connected with the base of each of the flappers is the branch of a main band extending to the base of the otolites, the nature of which seems yet problematical. Kowalevsky calls this band a nervous band, without further hesitation. Yet this band is capable of contraction and expansion, and I am more inclined to consider it with Kölliker a mere muscular band, although Fol describes what he supposes to be true a nervous system in addition to the muscular band. This nervous system I have been unable to trace in the young of any of the Ctenophoræ I have examined.

**SENSITIVE BULB.**—The sensitive bulb is formed from the outer embryonic layer, which has formed the outer wall and the locomotive flappers. It consists at first of a mere rising of a part of it and a rapid accumulation of small cells (Pl. II, fig. 20) in the middle of which four granules appear; these are little by little isolated and pushed off within the rapidly rising clear sphere, as fast as new

ones are formed; the clusters of granules eventually unite to form a central isolated cluster, the granules are constantly increasing in number; their function is as yet very problematical. From the position of the otolites they are evidently connected with the movement of the locomotive flappers and any disturbance felt by it is at once communicated to the locomotive flappers by the muscular bands connecting each row with the base of the otolite. Fol attempts to show that the outer envelope of the otolites consists originally of four parts, and is homologous to the locomotive flappers. It is undoubtedly formed from the same embryonic layer, but the youngest stages observed, both by Kowalevsky and myself, showed no trace whatever of the sectional character, which is developed later. The suspensors of the otolites are also developed quite late, and their origin is still imperfectly understood. I have in some of the very young stages observed very clearly within the envelope of the otolites vibratile motion, at a time when the locomotive flappers were still immovable, which may have been the first trace of the suspensors of the otolites. I afterwards looked in vain in subsequent stages for similar vibratile cilia, but could never trace them nor any movement in the otolites not connected with motion of the locomotive flappers.

I can hardly attribute to any of the organs situated at this pole, the function of an organ of smell, as has been suggested for the circumscribed abactinal area. From the fact that the anal opening is situated there we are led to assume that the discharge of the contents of the chymiferous cavity is accompanied with more than usually rapid ciliary motion; the only means of throwing off from the surface of the Ctenophore the contents of the digestive cavity, as they are cast out, is by the motion of the fringes of the abactinal apparatus.

CHANGES OF FORM IN YOUNG.—In my Catalogue of the North American Acalephæ I have already given the principal stages now to be described, from the first appearance of the lateral chymiferous tubes, until the main chymiferous tubes have become somewhat branching as in the adult. The changes now taking place are almost entirely limited to the growth of the chymiferous and of the lateral tubes, and the increase in length of the locomotive flappers. The chymiferous cavity has at first the shape of an elliptical cavity (Pl. II, fig. 26, *w*) which eventually forms loops of different sizes, extending only half-way down the spherosome (Pl. III, figs. 6, 10). The lateral tubes, like the chymiferous tubes, are at first large pouches, but they very fast become elongate narrower tubes. In the changes they undergo (Pl. III, figs. 6-10), by the gradual contracting of the

large pouches forming the chymiferous tubes, they become better and better differentiated (Pl. III, figs. 13-20, following), at the same time pushing their way down, and towards the actinostome, and becoming more and more narrow till they nearly reach it. At the same time the rows of locomotive flappers keep pace with the increase in length of the chymiferous tubes. The partial symmetry of the genus is clearly indicated in the younger stages, not only by the presence of the lateral tubes, but also by the unequal development in the length of the chymiferous tubes, the tubes nearest to the lateral tubes remaining the shortest till long after the connection of the chymiferous and of the lateral tubes to form a circular tube has taken place. By the time the longitudinal chymiferous tubes reach the actinostome they begin sending out branches at the abactinal part (Pl. III, fig. 20) which increase in number and length (Pl. III, fig. 21), the primary branches sending out lateral branches (Pl. III, fig. 22) as in the adult full grown specimens (Pl. III, fig. 24).

The abactinal fringed apparatus (the circumscribed area) is in the younger stages a mere circular ring (Pl. III, figs. 12, 14, 18) on each side of the base of the sensitive bulb; subsequently four folds are developed at the inner extremity, these gradually become the fringed edges of the sensorial apparatus (?) existing in the adult above the anal opening.

The brilliant phosphorescence which can be generated by the least shock to the jar in which Ctenophoræ are contained is perhaps more striking in *Idyia* than in any other genus of Ctenophoræ found on our coasts; although we know now something of the nature of the phosphorescence of a few marine Invertebrates from the observations of Panceri, who has plainly traced it to the secretion of special glands, yet when we find the same phosphorescence equally as brilliant in eggs of Ctenophoræ as in the adults, even in stages in which the masses of segmentation can still be counted, we have evidently not yet reached the solution of the true nature of this phosphorescence. The whole embryonic mass becomes brilliantly phosphorescent when the least shock is given to the jar in which the eggs are kept.

## PLEUROBRACHIA RHODODACTYLA.

*Pleurobrachia rhododactyla* AGASS. Mem. Am. Acad., IV, p. 314, 1849.

IN *Pleurobrachia*, as far as the earliest changes of the egg and the embryo are concerned, it is merely necessary to refer to the explanation of the Plates which will give a sufficiently full description of the different stages of segmentation of the yolk and of the formation of the embryo. It would be almost a verbal repetition of the processes described in *Idyia*. The segmentation and subsequent stages are somewhat more rapid in *Pleurobrachia* than in *Idyia*, the egg passing through the changes represented in Pl. IV in less than twenty-four hours, and in about three, four or five days the changes figured on Pl. V are gone through, the corresponding stages in *Idyia* develop somewhat more slowly. The difference in proportion between the outer envelope and the yolk mass (Pl. IV, fig. 1) has already been alluded to.

We have a perfect repetition in *Pleurobrachia* of the first appearance of the segmentation (Pl. IV, figs. 2-4) described for *Idyia*, as well as of the first segmentation into two, then into four spheres (Pl. IV, fig. 5), into eight spheres (Pl. IV, fig. 9), with this difference that the second spheres are proportionally smaller than they are in *Idyia*. We trace the formation of the actinal ring of small spheres (Pl. IV, figs. 10-20) from the actinal part only of the eight primitive spheres, and the gradual spreading of these small spheres (Pl. IV, figs. 21-32) so as to cover the large yolk spheres, to form an outer embryonic layer as contrasted with the inner enclosed yolk mass, leaving at first a portion of these spheres uncovered (Pl. IV, fig. 31), finally enclosing the inner yolk mass completely. Through this, as in *Idyia*, the outlines of the original eight yolk spheres can be indistinctly traced (Pl. IV, figs. 34, 35). As in *Idyia* we have very early (Pl. IV, figs. 9, 10) two axes developed, a vertical axis with an actinal and an abactinal pole, and a longitudinal axis, but no anterior or posterior extremity; this is the case in all *Ctenophoræ*. The walls of *Pleurobrachia* are formed as in *Idyia*; we have at an early stage very stout walls (Pl. IV, fig. 36), a marked depression at the abactinal pole, and a rapid accumulation of cells at the actinal pole, pushing their way into the inner yolk mass, and forming at that pole a marked depression, the walls of which soon form a shallow depression (Pl. IV, fig. 36) and gradually a well defined digestive cavity (Pl. IV, fig. 37). At about this stage the large yolk masses are well separated from the outer envelope;



a depression is formed at the abactinal pole, from the centre of which a prominence soon rises, the first trace of the sensitive bulb which now develops rapidly and soon the outline of the embryo is completely altered (Pl. IV, fig. 45, Pl. V, fig. 1).

As early as the stage represented in Pl. IV, fig. 37, we find traces of the future position of the locomotive flappers indicated by the accumulation of the cells of the body wall near the abactinal pole. The position of this thickened part of the wall is well shown in Pl. IV, figs. 43, 45. In Pl. V, fig. 1, there is as yet no sign of the flappers, which are seen only in the next stages (Pl. V, figs. 5, 6), as short, stiff, triangular points, perfectly immovable. These form the base of the flapper, which as it elongates becomes more and more movable, and splits up into several parts; the length of these flappers is in the young stages, entirely out of proportion to the size of the embryo (Pl. V, figs. 19-27); they are in their earlier stages within the egg case their principal means of locomotion. It is only subsequently, just before the escape of the embryo from the egg, when the oral part of the young Ctenophoræ is proportionally much more developed than it is in the adult, that the expansion and contraction of the actinal portions of the spherosome (Pl. V, fig. 30) materially assists in guiding the movements of the young. The thickened walls forming the base of the locomotive flappers are placed at the base of a broad swelling (Pl. V, fig. 1), which soon projects beyond the general outline of the spherosome (Pl. V, figs. 5, 6) and forms a distinct knob (Pl. V, figs. 8, 11), and in the next stage a sort of handle to the body of the young Pleurobrachia (Pl. V, figs. 10, 12, 13). These knobs are the origin of the long fringed tentacles; they increase rapidly in length in the subsequent stages (Pl. V, figs. 14, 21, 25, 30), and sometimes while still within the egg, a few branches are sent off from the main trunk of the tentacles; after the escape of the young from the egg they rapidly increase in number as fast as the tentacle lengthens, and become while the young Pleurobrachia is still quite small the graceful tentacles so characteristic of the genus.

The locomotive flappers do not increase greatly in number while the young is within the egg; there are but eight or nine pairs in each row. The only changes they undergo during growth are their increase in length, and the gradual separation of the adjoining rows of flappers, so as to form eventually the eight independent rows of flappers found in the adult. The rows are reduced in the young to four double rows (see Pl. V, figs. 5-30).

The formation of the sensitive bulb and otolites is readily followed from its first

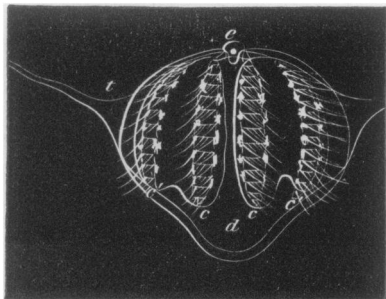
stages (Pl. IV, fig. 45), when the wall of the abactinal pole of the embryo is only a thickening, at the inner edge of which are formed four independent, distinct granules (Pl. V, figs. 1-3). These granules gradually approach with the rising of the sac till they unite and form suspended within it a cluster of four balls (Pl. V, figs. 8-10), to which additional granules are constantly added from the generating base of the otolithic sac (Pl. V, figs. 20-30). The digestive cavity, at first a mere inverted sac (Pl. V, fig. 1), gradually pushes its way towards the abactinal pole by the extension of the aboral part of the walls (Pl. V, figs. 5, 6), which forces its way between the abactinal central space of the large yolk cells, thus forming at an early age an ellipsoidal digestive cavity, from which has been formed as a diverticulum a chymiferous cavity; this little by little pushes its way to the abactinal wall of the spherosome (Pl. V, figs. 5-8). The increase of the base of the tentacles, and the extension of the digestive cavity have taken place at the expense of the yolk mass; about at the same time, exactly as was the case in *Idyia*, the connecting gelatinous tissue has commenced to form near the actinal extremity, at the expense of the central yolk mass. With the increase of this the walls of the digestive cavity of the chymiferous cavity become more and more movable, so that in the stage of Pl. V, figs. 19-29, the mobility of the digestive cavity has become very considerable, and the flattening of the spherosome shows in the narrow, compressed, digestive cavity a principal characteristic of the genus (Pl. V, figs. 22, 24). The interlacing of the cells of the body walls, at first seen only near the actinal pole, extends to the base of the tentacles (Pl. V, fig. 23). The central yolk mass is little by little reduced to a few of the large masses; at the expense of these the chymiferous tubes have developed, as diverticula of the chymiferous cavity, itself a diverticulum of the digestive cavity (Pl. V, figs. 22, 29<sup>a</sup>). The abactinal part of the chymiferous tubes becomes isolated from the body wall substance, at the expense of the yolk cells of the abactinal part of the embryo forming the funnel leading to the anal rosette. The last traces of the yolk cells to disappear are those surrounding the short chymiferous tubes placed between the base of the tentacles.

## MERTENSIA OVUM.

*Mertensia ovum* MÆRCH. In Nat. Bid. til Besk. af Grönl., 1857.

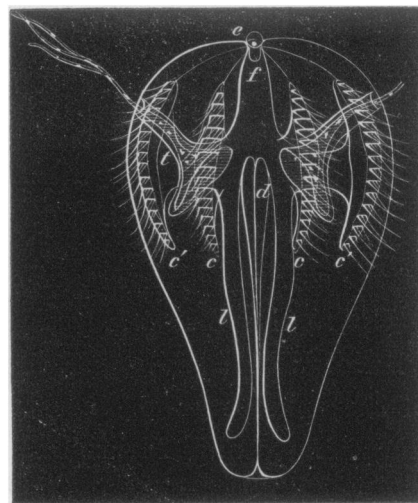
THE only other genus of the Cydippidæ of which I have examined the young is *Mertensia*; these young stages I have already sketched in my North American *Acalephæ*.<sup>13</sup> As I have nothing specially new to add I refer to the figures

Fig. 1.



given there, and insert two of them here for the purpose of showing the coincidence of their development with that of *Pleurobrachia*. The only point of difference worthy of notice is the great length of the bands of locomotive flappers as compared to *Pleurobrachia* (fig. 1). This is a generic distinction early appearing in the young *Mertensia* at a stage when the tentacles are as yet but simple long threads. The brilliant orange pigment spots are very prominent along the rows of locomotive flappers. In the youngest stages observed there were already eight rows of locomotive flappers. The actinal extremity is quite short compared to the rest of the spherosome; in *Pleurobrachia* when the flappers have attained the same degree of development, the actinal part of the spherosome below the locomotive flappers occupies more than one-half of the whole spherosome. There is nothing to be mentioned either with regard to the development of the lateral tubes, the increase of the locomotive flappers, the formation of the chymiferous tubes, of the lateral tubes, or of the growth of the tentacles which differs materially from what has been described in *Pleurobrachia*. The tentacular apparatus remains within the abactinal part of the spherosome (fig. 2) and does not extend towards the actinal regions as in *Pleurobrachia*.

Fig. 2.



<sup>13</sup> AGASSIZ, ALEXANDER. North American *Acalephæ*, 1865, p. 27, figs. 30-37.

Lettering of cuts of young *Ctenophoræ*; *d*, digestive cavity; *a*, anal rosette; *t*, tentacle; *c*, long ambulacral tube; *c'*, short ambulacral tube; *e*, eye speck; *f*, funnel; *o*, ambulacral cavity; *l*, lateral tubes; *n*, lobes of spherosome; *c'* is at first the longest tube and *c* the shorter.

Fig. 1. Young *Mertensia* seen from the broad side (diacæliac) with simple tentacles, greatly magnified.

Fig. 2. Young *Mertensia*, in which the tentacular apparatus (*t*) is isolated, the lateral tubes (*l*) are present, the chymiferous tubes (*c'*) are circumscribed and the main branches of the ambulacral system have lost the character of pouches; seen from the broad side (diacæliac).

## BOLINA ALATA.

*Bolina alata* AGASS. Mem. Am. Acad., iv, 1849.

THE changes undergone during growth by the preceding species have not been marked by any great variation of outline. Neither in *Idyia*, *Pleurobrachia* nor *Mertensia* were the earliest stages so different from the adult that mistakes regarding their systematic position could be made. The young of these genera differ only quantitatively from the adult. In *Bolina*, on the contrary, and in other allied Ctenophoræ the morphological changes are very great, and it would indeed puzzle the most accurate systematist to recognize in the early stages of some of the Mnemiidæ the young of well known genera. We cannot say that there is a metamorphosis in the ordinary sense of the word, as supposed by Gegenbaur, but there certainly are remarkable changes, such as the almost total suppression of the tentacular apparatus, the development of auricles, of lobes, with their complicated winding chymiferous tubes, which alter radically the appearance of the Ctenophoræ at successive periods of growth, and present between the younger and the older stages differences usually considered as of great systematic value. As I have already given in detail the earliest phases within the egg of two species (*Bolina* does not differ in its early development from the genera described) I will limit my remarks on *Bolina* to the changes of form which characterize the growth of the embryo after it has attained one of the corresponding stages already described for *Pleurobrachia*.

Up to the time the young *Bolina* escapes from the egg its resemblance to *Pleurobrachia* is so great that were it not for the compression in different planes, of the spherosome of these two genera, it would be exceedingly difficult to distinguish a young *Pleurobrachia* from a young *Bolina*. M'Crady was the first to show the close resemblance between *Pleurobrachia* and *Bolina* during the tentacular stage of the latter. In *Bolina* the tentacles are placed at the extremities of the longitudinal axis, and the large digestive cavity of *Pleurobrachia* is already replaced in this early stage by narrow chymiferous tubes which soon become an excellent guide for distinguishing readily the young of these two genera (fig. 3).

Fig. 3.

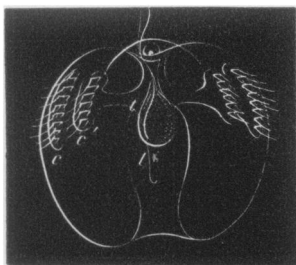


With advancing age the young *Bolina* undergoes changes of shape similar to

Fig. 3. Young *Bolina*, greatly magnified, immediately after the escape of the young from the egg; seen from the narrow side (diacoeliac).

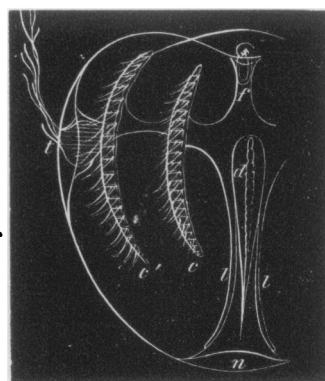
those already described in *Idyia* and *Pleurobrachia*. The outline becomes more elongated; the lateral tubes, at first simple diverticula from the main ambulacral

Fig. 4.



tubes, gradually push their way through the gelatinous mass of the spherosome along the flattened ends of the coeliac cavity (fig. 4) till they extend to the level of the actinal opening (fig. 5). At this stage a difference in the rate of growth of

Fig. 5.



the ambulacral tubes becomes apparent, the tentacular ambulacra growing more rapidly, and when they reach the bottom of the spherosome they bend towards each other

(fig. 6) and finally join (fig. 7) forming thus the first connected loop, enclosing, in the adult *Bolina*, the complicated winding tubes of the short pair of chymiferous canals of the actinal lobes. The actinal part of the spherosome at the same time rapidly projects beyond the level of

Fig. 6.

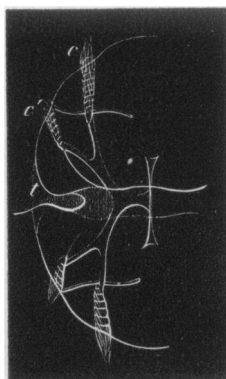
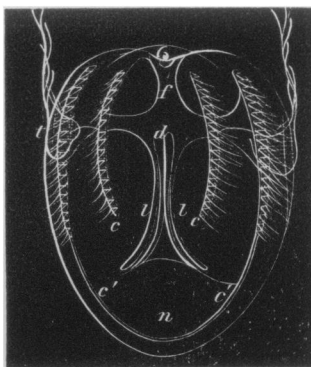
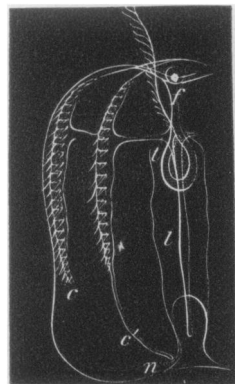


Fig. 7.



the actinostome, the young *Bolina* having at that stage well marked simple lobes, but as yet no auricles and at the same time still having highly developed tentacles like those of *Pleurobrachia* (figs. 8, 9).

Fig. 8.



Greater changes are yet to take place before we can trace the rudiments of all the parts of an adult *Bolina*. The long tentacular chymiferous tubes do not remain regularly arched forming a simple curve; they bend towards the vertical axis at the level of the actinostome, the indentation is gradually changed into a loop, the spherosome at the same time projecting beyond the general level and finally forms a rudimentary auricle

Fig. 9.

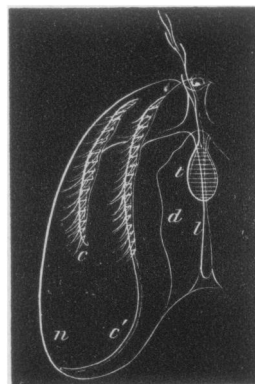


Fig. 4. Same as fig. 3, seen from the broad side (coeliac).

Fig. 5. Young *Bolina*, in which lobes begin to appear; somewhat more advanced than in fig. 4.

Fig. 6. Somewhat more advanced stage than fig. 5; seen from the actinal side; the tube *c'* has nearly completed the circuit round the actinostome.

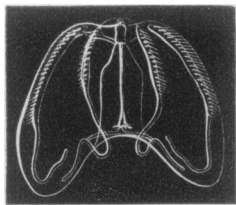
Fig. 7. *Bolina* somewhat older than fig. 6; the tentacular ambulacra have united; the lobes (*n*) project well beyond the end of the actinostome; seen from the narrow side (diaceliac).

Fig. 8. Diaceliac view of *Bolina*, somewhat younger than fig. 7; seen from the broad side.

Fig. 9. Fig. 7 seen from the broad side.

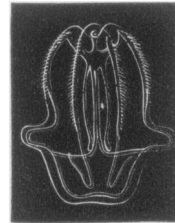
(fig. 10). From the angle of the auricle a branch of the chymiferous tube soon pushes its way through the gelatinous mass towards the coeliac cavity and makes a junction with the lateral tubes, exactly as we have seen it in the case of *Idyia*.

Fig. 10.



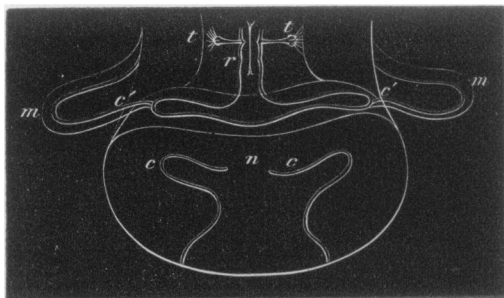
In the meantime the short ambulacra have also been increasing in length; they soon reach to the lower end of the lobe, where they make a sharp angle, turn upward (figs. 11, 12) and form thus the beginning of the complicated system of windings which we find in the lobes of the adult *Bolina*

Fig. 11.



(Pl. III, fig. 27). During the later stages of growth the tentacular apparatus has been shifting its position, the opening coming nearer and nearer the level of the mouth, the tentacular bulb lengthening in proportion, and finally appear-

Fig. 12.



ing like a long, narrow rod, with a slight swelling at the extremity, from which the remnants of the threads of the tentacles are suspended. The only changes now necessary to transform this young into an adult *Bolina* are changes of quantity. The apparent difference in the mode of growth of the lateral and longitudinal tubes is entirely

done away with in subsequent changes; we find that the short ambulacra are in reality the lateral ambulacra, though at first they are more rapid in their growth than the others; they are afterwards outstripped by the rapid increase in length of the longitudinal tubes; it must be remembered that in this genus the flattening of the spherosome takes place in different planes from *Idyia* and *Pleurobrachia*. The young *Bolina* has now attained a condition in which it will be very easy to recognize the different parts of the adult, if compared in homologous positions.

Fig. 10. Young *Bolina* at time of the first appearance of the auricles; seen from the broad side.

Fig. 11. *Bolina*, in stage of fig. 10; seen from the narrow side.

Fig. 12. Fig. 11 seen from the actinal side, more magnified; *r*, circular tube; *m*, auricles.

## SYSTEMATIC POSITION AND AFFINITIES OF CTENOPHORÆ.

THE question of the systematic position of the Ctenophoræ can now, thanks to the greater knowledge we have of their embryology, be treated more intelligently. The position taken by Vogt who follows Quoy in removing them from the Acalephs altogether, and associating them with the Mollusks on account of the apparent bilaterality so strongly developed in some families (Cestum, Bolina and Mertensia), seems now untenable. The nature of their relations to Echinoderms, Polyps and Acalephs as well as the general relations of the Cœlenterata to Echinoderms may be discussed again, especially as having an important bearing not only on the value of the Cœlenterata as a primary division of the animal kingdom, but also on the limits of Radiates, and the possible affinities of the Sponges and Cœlenterata suggested by Haeckel.<sup>14</sup> A still more important point developed from this embryology is its connection with the Gastræa theory of Haeckel,<sup>15</sup> for which he claims that it will supplant the Type theory, and give us in its place a new system based upon the homology of the embryonic layers and of the primitive digestive cavity. Haeckel attempts, in his Gastræa theory, to find an explanation for the natural development of species from a purely mechanical cause, and has been bold enough not only to name, but also to figure, the primitive ancestor from which all types of the animal kingdom have been developed! This unknown ancestor, he says, must have been built much like his gastrula, only another name for what has long been known to all students of Invertebrates as the Planula of Dalyell. Haeckel would lead us to believe that this gastrula is a newly discovered embryonic stage; all he has done with reference to it, is to recall the existence of planulæ among Sponges which had previously been discovered by N. Miklucho Maclay.<sup>16</sup> Since the publication of Haeckel's article, his special interpretation of fanciful affinities and homologies existing only in forms conjured up by Haeckel's vivid imagination, have been sufficiently criticised by Metschnikoff,<sup>17</sup> so that until we know something more of the development of Sponges we may leave the discussion of their affinities with Cœlenterates out of the question, in spite of the ingenious arguments advanced to support Leuckart's views on the subject.

The existence of planulæ, the walls of which consist of an ectoderm and

<sup>14</sup> HÆCKEL, E. Die Kalkschwämme Berlin, 1872.

<sup>15</sup> HÆCKEL, E. Die Gastræa Theorie, Jenaische Zeitschrift ix, 1874.

<sup>16</sup> MACLAY, N. MIKLUCHO. Jen. Zeitschrift, iv, 1868.

<sup>17</sup> METSCHNIKOFF, E. Zur Entwicklungsgeschichte d. Kalkschwämme. Zeits. f. Wiss. Zool., xxiv, 1874.

entoderm, has been distinctly proved for *Acalephs*, *Echinoderms*, *Polyps*, *Worms*, *Arthropods*, *Tunicates*, *Mollusks*<sup>18</sup> and finally for *Amphioxus*, the papers of Johannes Müller, Krohn, Agassiz, Kowalevsky, Sars, Allman, Claparède, Kupfer, Metschnikoff and others, are too well known to need citation in this connection. So far we are in perfect accordance with Haeckel and cordially agree with him in his estimate of the systematic value of this early embryonic stage, whether we call it planula or adopt his later name of gastrula. But let us follow his subsequent steps and separate what is known from what is stated as known by Haeckel. It is known that the planula consists of an entoderm and of an ectoderm. It is known that the primitive digestive cavity is in the case of *Echinoderms*, of *Ctenophoræ* and of some *Discophoræ*, formed by the turning in of the ectoderm, so that the wall of this primitive cavity, is, in their case at least, invariably formed by the ectoderm. It is known on the other hand that in *Actiniæ*, in *Worms*, in *Hydroids*,<sup>19</sup> this primitive digestive cavity is hollowed out of the inner yolk mass of the embryo, and has its walls formed by the entoderm. We must lay great stress on this point, which is alluded to by Haeckel as of no consequence,<sup>20</sup> for this seems to us to destroy the very base of his argument. If the gastrula can in one case, and in such closely allied classes as *Actiniæ* and *Hydroids* on one side, and *Echinoderms* and *Ctenophoræ* on the other, be built so differently that in the first case the walls of the primitive cavity are formed by the entoderm, and in the other of the ectoderm, what becomes of all his subsequent generalizations of the value for systematic purposes of these two layers? The distinction of entoderm and ectoderm is, as Haeckel himself acknowledges, and as is sufficiently shown by Kowalevsky, of the greatest anatomical value, yet how is it possible that these differently constructed planulæ should have the genetic connection claimed for them by Haeckel, if in their very embryonic stages the differences are of so radical a nature that according to the very theory of embryonic layers so strongly insisted upon by Haeckel, they could have no possible relation, the one being a product of the entoderm, the other of the ectoderm, the two primitive embryonic layers.

It is not known as is stated by Haeckel, that the walls of the primitive digestive cavity are invariably formed of the entoderm, and when Haeckel states the result (the gastrula) to be the same whether formed by the ectoderm or entoderm he states what is known to be exactly the contrary. It is not known as is stated by Haeckel, that the mere fact of a planula fixing itself by one extremity or not,

<sup>18</sup>LANKESTER, E. R., On the primitive cell layers of the Embryo. *Ann. Mag. N. H.*, Feb., 1873.

<sup>19</sup>FOL, H. Die erste Entwicklung d. Geryonideneies. *Jen. Zeitsch.*, vii, p. 471.

<sup>20</sup>HAECKEL and LANKESTER both seem to think that because the result is a similar form it must be homologous.



will in one case lead to a radial type in another to a bilateral type. What becomes of all the free swimming Embryos of Echinoderms, of Acalephs of Polyps? Are they bilateral? It is true Haeckel is obliged to suit his theory, to consider the Echinoderms as an aggregation of individuals but he has not the countenance of a single zoölogist whose opinion on Echinoderms is of any value; when he says that Sars, whose knowledge of the development of Echinoderms was so accurate, agreed with his peculiar views, we can only reply that his agreement must be based upon a misunderstanding. We have equally as many radial and bilateral types developed either from fixed or from pelagic gastrulæ and to cite this as a *causa efficiens*, the mechanical reason of the genetic descent of all radiates from a fixed gastrula, and of all bilateral types from a free swimming one, is simply fantastic. How is it that so many Actiniæ and Acalephs have their radiate structure developed long before they become fixed? It is not known that the embryonic layers of Acalephs are truly homologous to those of the higher Vertebrates. Huxley simply speaks of their bearing the same physiological relation to one another, but until we know the gastrula of other Vertebrates than Amphioxus it is idle to talk of the continuity existing between the Ontogeny of Amphioxus, and the remaining members of the Vertebrate branch, and to say that hence there is *no doubt left* that the ancestors of the Vertebrates must have passed through in the beginning of their development the gastrula form! Neither Haeckel nor any one else has seen this; it is a pretty hint which may or may not be proved.

Considerable confusion arises in Haeckel's classification from his adopting at one time as of primary importance the development of the cavity of the body and making it the main point in his phylogenetic classification, while previously the relations of the phylum to Protascus and Prothelmis (names he gives to the unknown ancestors of the radial and bilateral types) formed the basis of his classification. This places him in the awkward predicament of having a phylum of the animal kingdom (the radial) which has lost the capacity of forming a body cavity, and yet its descendants have in some unaccountable manner (entirely against the rules of Haeckel's theory) managed to get one by some unexplained method. We do not see how it can be so confidently stated by Haeckel that Echinoderms have lost their original central nervous organ; there is no proof whatever of its once having existed. There is, as yet, no proof whatever that the organs of sense (which, as had already been so often insisted upon by Agassiz, are not homologous in the different branches of the animal kingdom) have the same phylogenetic origin.

When Haeckel says that the mouth of Echinoderms is not homologous to the primitive mouth we can only refer him to the memoirs of Müller, Metschnikoff and myself on Echinoderm embryos for proof to the contrary.

There seems no doubt, as Haeckel insists, that to the majority of zoölogists of the present day the idea of type is a very different one from that of type as understood by Baer and Cuvier. The probability of their original community of origin is hinted at from the many so-called intermediate forms both living and fossil which, though we may enroll them either in one great branch of the animal kingdom or another, yet show that we can no longer consider the great types of the animal kingdom as closed cycles, but must hereafter regard them as holding to one another relations similar to those which the remaining categories of our systems have to one another. This change has principally been brought about by a better knowledge of the embryology of a few well known types.

But what becomes of all the assumptions of Haeckel which form the basis of his *Gastræa* theory? They are totally unsupported, and with their refutation must fall his theory; it can only take its place by the side of other physiophilosophical systems; they are ingenious arrangements laboriously built up in the interest of special theories, which fall to the ground the moment we test them by our actual knowledge. That the time has not yet come for embryological classifications, the attempts of Haeckel plainly show, for they are in no ways in advance of the other embryological classifications which have preceded them; we get new names for somewhat different combinations, but a truly scientific basis for a classification based upon the value of embryonic layers is at present impossible; such attempts can be only speculations to be proved or disproved on the morrow.

What Haeckel substitutes in place of the accepted types of the animal kingdom is simply another view of these same types, and his *Gastræa* theory is in no danger of upsetting, at present at least, zoölogical classification as now understood. Indeed if we need an ancestor for our phylum why not at once go back to the cell? There we have a definite starting point, a typical element which underlies the whole of the animal kingdom and which forms the walls of Haeckel's gastrula. Then we shall all be agreed and when we frankly state that all organisms are derived from a primitive cell and from its subsequent increase, we come within the range of positive knowledge, but we are unfortunately as far as ever from having for that reason been able to trace a mechanical cause for the genetic connection of the various branches of the animal kingdom. We must meet the direct issue raised by Haeckel,—that such a genetic connection either does or does not exist,—by

repeating what has so often been said by others, this genetic connection may exist but we have at present no proof that it does exist and at any rate his gastræa theory does not bring us any nearer to a mechanical explanation of such a genetic connection however probable it may be.

We have already referred while describing the segmentation (Pl. I, figs. 17, 24, 25) to the early date at which we could distinguish a vertical axis through which we can pass two planes, at right angles, which are distinctly indicated from this time forward; the vertical axis we may call the actinal axis, while the two planes can be called the cœliac and diacœliac, the cœliac plane including the abactinal rosette and passing at right angles to the plane in which are included the lateral tubes. The lateral tubes with the abactinal rosette can alone give us the position of homologous chymiferous tubes in different genera. These planes determined, we find that the long tubes of *Pleurobrachia*, *Mertensia*, *Idyia*, *Bolina*, *Lesueuria*, etc., are by no means homologous. In *Pleurobrachia* and *Mertensia*, the diacœliac plane is the longitudinal plane while in *Bolina* and *Lesueuria* it is the transverse plane, consequently the long tubes of *Mertensia*, or rather the homologues of the tentacular tubes of *Bolina*, are the shorter tubes placed on each side of the tentacular system. As the lateral tubes are always in the same plane with the tentacular pouches, in *Bolina*, *Lesueuria* and *Mertensia*, we find no difficulty in placing *Idyia*, although destitute of tentacles, in an homologous position with other tentacle-bearing genera by taking as our guide the relation of the lateral tubes to the abactinal rosette. The recognition of these very definitely fixed planes and axes naturally leads us to the views of Agassiz and of Fritz Müller regarding the radial plan of structure of Ctenophoræ. These views differ but little, and, as we shall show, depend for the agreement of their minor points on structural features quite subordinate to the plan of radiation acknowledged as typical of Ctenophoræ both by Agassiz and Fritz Müller.

Fritz Müller<sup>21</sup> considers the Ctenophoræ as biradiate animals in opposition to the views of those who call them either completely radiate or bilateral animals. As far as embryology can throw any light on the question of the number of (rays) spheromeres of which Ctenophoræ are composed, it is difficult to answer positively; if we take the early stages of *Idyia* and consider the number of spheromeres to be denoted by the rows of locomotive flappers, then there are eight spheromeres; if we take into account only the chymiferous pouches there are but four. In *Pleurobrachia* if we take the locomotive flappers as our guide there are four, and

<sup>21</sup> MÜLLER, FRITZ. Ueber die angebliche bilateral Symmetrie der Rippenquallen. Archiv f. Naturg., 1861.

if we consider the chymiferous pouches there are but two. So that we find in Ctenophoræ (as we find Echinoderms with a varying number of rays) not only genera with four or with eight rays, but also genera with but two spheromeres. We doubt if the introduction of the word spheromere has tended to define accurately our notions of the plan of structure not only of Ctenophoræ but also of other radiates. The presence in Echinoderms of a single digestive pouch, of an œsophagus, a digestive cavity, an alimentary canal, an anal opening, plates forming an abactinal system, or in Ctenophoræ of an abactinal rosette, of the cœliac openings, of lateral tubes, tentacles and of a circular ring, tend to confuse our ideas from the association of these simple or single organs with a radiate structural plan, and naturally introduce into the comparison with other branches of the animal kingdom questions of symmetry, of anterior and posterior extremities, of oral and aboral poles, which completely overshadow, as in Ctenophoræ, the radiate structure. Whatever planes we imagine, in dividing Ctenophoræ, passing through the actinal axis (from the actinal opening to the abactinal system) either at right angles to the lateral tubes or through them, we do not obtain similar spheromeres from the subdivision into four, it is only when we limit the number of spheromeres to two, that a symmetrical division can be made by an actinal plane passing at right angles to the plane including the lateral tubes. Yet the embryology of *Idyia* at least would show that in that genus we must, even taking the chymiferous pouches as our guide, admit the presence of four spheromeres. So that although we can admit and do admit an actinal and an abactinal pole, a cœliac and a diacœliac plane, yet we cannot admit an above and a below which are the essential features of a bilateral animal. The presence of a madreporic body in Echinoderms fixing the position of one extremity of the cœliac or diacœliac axis does not yet make an above or a below in the sense in which we understand it of bilateral animals.

When Leuckart established his sub-kingdom of Cœlentera, which, up to the present day has received such a general recognition, while the views which have always been maintained by Prof. Agassiz, regarding the affinities of Echinoderms and Ctenophoræ have met with but little favor, comparatively little was known of the embryology of the classes which he united, and still less of the Echinoderms which he separated from them. Since that time the wonderful researches of Müller into the embryology of Echinoderms, with the subsequent modification of his views by Metschnikoff and myself have been published. Since that time the development of Polyyps has been unfolded more especially by the brilliant memoirs

of Lacaze Duthiers,<sup>22</sup> and in no department of marine animals has there been a greater number of memoirs on Embryology than in the class of Acalephs. We are therefore in a position, now that the embryology of Ctenophoræ is well known, to renew the discussion of this subject again. As I have already stated in my paper on *Balanoglossus*, it seems hardly necessary to refute Haeckel's assumption of the composite nature of Echinoderms. As Metschnikoff well remarks, any one who has ever traced the development of an Echinoderm could not hold such a view for an instant. This digression is necessary as we have shown that Ctenophoræ have, like all Echinoderms, a digestive cavity formed in precisely the same manner, and that from this digestive cavity are formed as diverticula, the chymiferous tubes which correspond in every respect with the water tubes of the Echinoderms. Metschnikoff<sup>23</sup> has lately taken the same view in an interesting memoir on the development of Acalephs and Siphonophoræ. This is the same view which I formerly proposed on embryological grounds,<sup>24</sup> and reiterated in the Catalogue of N. A. Acalephæ and the history of *Balanoglossus*.<sup>25</sup> Here we must call attention to a marked difference between Acalephs and Polyps on one side, and Echinoderms on the other, that while in the former the connection between the digestive cavity and the water system always remains open, it is at one time disconnected in the Echinoderms, though it is eventually reopened through anastomoses of the water tubes. The anal opening holds in Ctenophoræ very much the same relation which it holds in Echinoderm larvæ, in which the water tubes are still connected with the primitive digestive cavity. When we find, as we do, that in Ctenophoræ as well as in Echinoderms, the primitive digestive cavity is formed by the inturning of the ectoderm, that in both classes the water system is developed as diverticula, from this digestive cavity, we fail to see how we can separate the Ctenophoræ from Echinoderms and place them with Polyps in a separate subkingdom of the animal kingdom. No one questions the relationship of Ctenophoræ to Acalephs yet from embryological data it would be more natural to associate Echinoderms and Ctenophoræ into one subkingdom characterized by the mode of formation of the water system as diverticula, forming eventually chymiferous tubes in both classes, and to associate the other Acalephs with the Polyps<sup>26</sup> where the chymiferous tubes and cavities are formed by the liquefac-

<sup>22</sup> LACAZE DUTHIERS, H. DE. Développement des Corailliaires, Archives de Zool. I, 1872, II, 1873.

<sup>23</sup> METSCHNIKOFF, E. Zeit. f. Wiss. Zool., 1874.

<sup>24</sup> AGASSIZ, ALEXANDER. Embryology of the Starfish, in Agassiz Cont. Nat. H. of U. S. V, 1865.

<sup>25</sup> AGASSIZ, ALEXANDER. History of *Balanoglossus*, Mem. Am. Acad., Vol. ix, 1873.

<sup>26</sup> See ALLMAN'S views on the position of the Ctenophoræ as contrasted to the Actinozoa. Trans. R. S. Edinb. xxvi, Pl. II, p. 466, 1871.

tion of the interior of the planula. Any one who will compare the figures of the embryos of starfishes (A. Agass. Embryol. Starfish, Pl. II, fig. 8) and Ctenophoræ (Pl. III, figs. 6-10; Pl. V. figs. 5, 11) at the time when the chymiferous tubes are reduced to mere diverticula cannot fail to be satisfied of their complete identity of plan. Metschnikoff has made, in addition to the homologies I have just recalled, a most interesting comparison between an Echinoderm larva and a Ctenophore; he shows that even in the adult Ctenophore the identity of plan is not destroyed and is carried out to the smallest details. The only point in which I would differ from him is in his comparison of the abactinal cœliac openings to the actinostome; he seems to forget that in Echinoderm larvæ what at first performed the part of anus and mouth eventually becomes the mouth alone, so that his figures should be reversed, and then the identity will be found complete between an Echinoderm larva (see A. Agassiz, Embryol. Starfish, Pl. III, fig. 6, and Pl. VII, fig. 8) with its œsophagus, digestive cavity, alimentary canal and its chymiferous pouch (water system) from which run the diverticula eventually to become the water tubes, and a Ctenophore (Pl. III, fig. 25) with its lateral tubes on the sides of the digestive cavity, (*g*) leading into the chymiferous pouches, *w*, branching into the chymiferous tube. The cœliac opening (Pl. III, fig. 45, *ca*) of the funnel he looks upon as representing the madreporic body, while I look upon them as the anal openings. In this view of the case, the Ctenophore is rather more in the embryonic condition of the Echinoderm larva, when the actinostome leading into the digestive cavity should perform at the same time the function of mouth and anus, which it occasionally does, although at other times the cœliac opening of the funnel seems to be the true anal opening, while according to Metschnikoff, it is the madreporic body, which performs the part of an anal opening. He says it only acts to introduce water into the system which is contrary to my observations.

I may here recall former statements<sup>27</sup> concerning the affinities of the Ctenophoræ, when describing some of the younger stages. It could only be after a careful comparison of Ctenophorous and of Echinoderm embryos, that undoubted evidence of their identity of plan might be obtained. The Ctenophoræ retain the permanently embryonic features of Echinoderm embryos, in which the water system is still connected with the digestive cavity. The formation of a funnel as a sort of alimentary canal, opening externally through the cœliac apertures at the abactinal pole, corresponds to the existence of a short alimentary canal in

<sup>27</sup> AGASSIZ, ALEXANDER. Ill. Cat. M. C. Z., No. 2, p. 12, 1865.

Echinoderm larvæ. The Ctenophoræ are from their embryology, more closely related to the Echinoderms than to the other Acalephs, and it seems natural to separate the Acalephs into two orders, the Ctenophoræ characterized by the presence of locomotive flappers and the Medusidæ, including the Discophoræ, and Hydroids.

I have been unable to analyze several important embryological memoirs on Cœlenterata by Noschin (1865), E. and L. Metschnikoff, 1871, and by Kowalevsky, 1873, all unfortunately printed in Russian, of which abstracts have appeared in Leuckart's *Berichte* or in the *Göttinger Nachrichten*. The Memoir by Kowalevsky (1873) is, to judge from the Plates, of great embryological value. I can only regret that he, in common with several other Russian naturalists, insists on publishing so many of their capital papers in Russian, and leaving their colleagues completely in the dark regarding their investigations. These Russian embryologists have followed Agassiz in his opposition to the interpretation of the Cœlenterata as promulgated by Leuckart, and so generally accepted by German and English naturalists.

EXPLANATION OF THE PLATES.

PLATES I-V.



## PLATE I.

*Idyia roseola.*

1. Fecundated egg of *Idyia*, 0.5<sup>mm</sup> in diam. *e*, transparent envelope; *y*, yolk mass; *c*, granular layer, the germinal layer.
2. First trace of segmentation; the germinal layer is concentrated (thickened) at one pole *c'*.
3. A depression is formed at one pole of the thickened germinal layer, between the two protuberances *c'c'*.
4. Somewhat more advanced than fig. 3; seen facing one of the protuberances.
5. The depression has penetrated farther into the yolk mass.
6. The protuberances approach one another while the groove penetrates the yolk mass.
7. The two yolk masses are distinct, but connected by a slight bridge.
8. The yolk masses are separated, but still retain an irregular outline.
9. The yolk masses have become regular preparatory to a second segmentation.
10. The segmentation into four has commenced by the indentation of the thickened germinal layer at one pole, in exactly the same manner as it passed from stage of fig. 3 to fig. 5.
11. The segmentation into four yolk masses is still farther advanced than in fig. 10; the germinal layer surrounding the yolk mass is at the pole opposite the connecting bridge.
12. Shows the mode of connection of the bridge between adjoining yolk masses, immediately preceding the stage following, in which there are four yolk masses (the bent dumb-bell state).
13. Yolk masses seen from the side. Segmentation into four yolk masses nearly completed, connected by bridges.
14. Yolk mass seen from the pole opposite to the bridge.
15. Showing the narrow bridge connecting the four yolk masses (the same as fig. 14).
16. A view of the dumb-bell state; fig. 11 seen obliquely; *b*, connecting bridge.
17. Commencement of the segmentation into eight; the process is the same as already described, only the four additional yolk masses are of smaller size.
18. The four yolk masses are nearly ready to separate; the bridge, *b*, is quite slender.
19. The four yolk masses are now arranged round a vertical axis; they each consist of a yolk mass *y* and a thickened embryonic layer *c''*, *c''*, at the pointed pole.
20. The germinal layer has increased somewhat in thickness.
21. The segmentation into eight, commenced in fig. 17, is somewhat more advanced; the view is taken facing the spheres of segmentation, from the pole passing through the cavity surrounded by the yolk masses.
22. Nearly in same stage as fig. 21 seen from the opposite pole.
23. The eight yolk masses are quite distinct (*a*, *b*, *c*, *d*).
24. The same seen in profile (*a*, *b*, *c*, *d*).
25. The yolk masses are somewhat separated and arranged in an ellipse round a vertical axis.
26. Somewhat more advanced than fig. 25, seen obliquely to show the connection of the masses. The germinal layer has increased in thickness at one pole. The yolk masses still consist of the same polygonal masses of which the original yolk mass was composed; the germinal layer also does not differ as yet from the layer of the earlier stages. The yolk cells of the larger mass remain essentially the same until the cells of the germinal layer nearly conceal them, while the cells of the smaller masses, after the segmentation into more than eight masses, assume a different structure.
27. End view of fig. 26.
28. Side view of yolk mass in which the actinal segmentation of the smaller spheres has commenced to form sixteen unequal masses; in figs. 28-30, corresponding to stage of fig. 10, corresponding masses have same lettering (*a*, *b*, *c*, *d*).
29. The small spheres are somewhat more advanced, still connected to the larger ones by a bridge.
30. End view of the yolk masses, segmentation about in state of fig. 29.

31. Yolk mass seen from the actinal pole, the masses are arranged round a vertical axis, each small mass forming a small overhanging projection, at the extremity of which the germinal layer is concentrating preparatory to a rapid segmentation, to be accomplished as in the earlier stages of segmentation.
33. Somewhat more advanced than fig. 31.
34. The eight small actinal masses have in their turn commenced to subdivide, passing through the dumb-bell shape.
35. Somewhat more advanced than fig. 34, seen obliquely.
36. Still more advanced than fig. 35; the small spheres are all distinct and a well marked nucleus exists in each of the small spheres; this becomes subsequently more prominent in figs. 38 and following.
37. The small masses at the actinal pole have undergone a farther segmentation.
38. The small masses form a narrow layer round the actinal pole.
39. The actinal layer has encroached somewhat more on the yolk masses.
40. About in stage of fig. 38 seen obliquely.
41. Somewhat more advanced than 40 seen from the abactinal pole; the actinal layer has reached nearly to the periphery, the large yolk masses have subdivided and have become wedge shaped, enclosing a shallow elliptical space within their proximal faces.
42. Somewhat more advanced than fig. 41 seen from the actinal side to show the mode of encroachment of the actinal germinal layer over the large passive yolk masses.
43. About in the same stage as preceding fig. seen in profile.
44. The large internal yolk masses have still farther subdivided, and have lost much of their former regularity; seen from the abactinal pole.
45. Seen in profile, the actinal layer has encroached over the internal yolk masses, beyond the equator; the space between the large yolk masses appears like a longitudinal fissure.
46. About in the stage of fig. 45 seen from the abactinal pole towards which the actinal germinal layer is gradually reaching.

## PLATE II.

*Idyia roseola.*

1. Shows the irregular mode of origin of the small spheres near the actinal opening.
2. Somewhat more advanced; both figs., 1, 2, seen in profile.
3. About in stage of fig. 2, seen from the abactinal pole.
4. Somewhat more advanced; seen in profile, the embryo has become somewhat cup-shaped.
5. The mulberry stage of the actinal germinal layer is very distinct round the actinostome.
6. About in the same stage as fig. 6, seen from the abactinal pole.
7. The germinal layer of small spheres has completely covered the large internal yolk masses still apparent in the preceding fig., and has left only a small part of the abactinal pole uncovered by them.
8. The germinal layer has in this stage completely surrounded the large yolk masses, which are only very indistinctly seen through the small spheres.
- 9, 10. Profile views of the embryo in which the actinal trench is quite well marked, but in which the actinal germinal layer is not as advanced as in the previous stages.
11. About in same stage, seen from the actinal pole.
12. Somewhat more advanced than fig. 11.
13. The embryo is depressed at the two poles, the small spheres of the outer germinal layer have become quite diminutive compared to their size in fig. 8; they form an outer envelope, through which the irregular, fatty yolk masses can be indistinctly traced.
14. First formation of locomotive flappers *v*, *v*, as accumulations of cells of the outer wall *c*, surrounding the internal yolk masses *y*. A slight depression, the future actinostome, is formed at *a*, accompanied by a very marked thickening of the outer wall at that point.
15. Somewhat more advanced than fig. 14; *o*, first trace of the otolithic sac also, formed as a thickening by the more rapid accumulation of the cells of the outer envelope at the expense of the inner yolk cells.
16. About in stage of fig. 15, the internal yolk masses somewhat more broken up.
17. Although the sensitive bulb and locomotive flappers are less advanced than in the preceding figures, the cells forming the wall of the actinal cavity have pushed their way nearly to the abactinal pole.
18. The same seen from the actinal pole; the actinal opening is already a well marked circular opening, *a*, the outer wall, *i*, is quite thin at the periphery and the internal yolk masses, *y*, still distinct.
19. In this stage the thickening of the walls for the locomotive flappers has been resorbed to form eight rows, each consisting of five rudimentary flappers. The upper flappers are mere stiff prolongations of the walls which little by little form a movable plate, as in the lower flapper.
20. The walls of the digestive cavity have become quite thick, forming a large inverted pouch, *g*. We also find in this stage the first trace of the otolites themselves formed from the granules of the outer wall.
21. The otolites and locomotive flappers as in fig. 20; the digestive cavity, however, is scarcely more advanced than in fig. 17.
22. First trace of the opening of the extremity of the digestive cavity leading into the water system.
23. About in stage of fig. 22, seen from the actinal side.
24. Seen from the abactinal pole to show the otolites, *o*, and the accumulation of small spheres from which the locomotive flappers are developed.
25. The embryo now enters into an important stage, in which we find the first trace of the pigment cells so characteristic of the genus. The sensitive bulb rises well above the outer wall as a transparent hemisphere, and the water system, *w*, is plainly seen as a small diverticulum at the extremity of the digestive cavity, *g*. At the same time the yolk masses, *y*, become subdivided and concentrated immediately around the outer wall and the digestive cavity, forming two layers, an inner more transparent mass surrounded by darker masses, between which and the outer wall the connecting gelatinous tissue, *t*, is formed at the expense of the inner nutritive yolk masses.

26. Somewhat more advanced than fig. 25; the gelatinous tissue has greatly increased, the inner yolk masses have retreated, and the water system, *w*, is quite prominent.
27. Different embryo; water system more advanced, connecting tissue less developed (figs. 25-27 in profile).
28. Seen from the actinal pole, nearly in stage of fig. 26.
29. The embryo has become quite elongated.
30. The same seen from the abactinal pole, lettering as before.
31. The walls of the digestive cavity have become more movable.
32. Fig. 33 seen from the actinal pole.
33. Oblique view of embryo to show the connecting gelatinous tissue formed at the expense of the inner nutritive yolk masses.
34. The difference between a coeliac and diacoeliac axis is quite marked, owing to the width of the digestive cavity and the size of the diverticulum of the digestive cavity, forming the water system, *w w*; seen facing the diacoeliac axis.
35. Seen facing the coeliac axis.
- 36, 37. Embryos somewhat older; the pigment cells have become smaller, but more numerous; seen facing the diacoeliac axis.
38. Seen facing the coeliac axis; the actinal extremity of the digestive cavity is armed with large, stiff cilia, which first appeared in fig. 34.
39. Embryo has become pear-shaped; seen facing the diacoeliac axis.
40. Seen from the abactinal pole, showing the rudimentary branches (chymiferous tubes) of the water system leading below the locomotive flappers.

## PLATE III.\*

*Idyia roseola.*

1. Seen from the actinal pole showing the shape of the actinal opening, the connecting gelatinous tissue *t*, and the yolk masses *y*.
2. About in stage of fig. 1, seen in profile (diacœliac).
3. About in stage of fig. 1, seen facing the cœliac axis.
4. Somewhat more advanced than figs. 2, 3. The yolk masses reduced to a triangular shaped body *y*.
5. (Diacœliac). The locomotive flappers have become quite long and very flexible, the otolites in this and stages immediately preceding completely isolated.
6. The connecting tissue of the abactinal part of the embryo has separated the upper portion of the four chymiferous pouches which now extend to the lower level of the locomotive flappers; their walls are forming by the differentiation of the yolk masses; these are reduced to two triangular shaped bodies on each side of the digestive cavity (diacœliac view).
7. Cœliac view of embryo somewhat more advanced than that of fig. 6.
8. Diacœliac view of embryo somewhat less advanced than the two preceding figures; shows the position and outline of the remaining yolk masses, *y*.
9. The chymiferous pouches have now a separate branch for each row of locomotive flappers, the yolk masses are reduced to a narrow cylindrical body, *y*, and small accumulations at the base of the chymiferous pouches; the pouches also lead outward through openings below the rosette, *ca*. The sensitive bulb and the otolites are quite well separated from the outer wall (cœliac view).
10. The chymiferous tube, *ch'*, *ch''*, as well as the lateral tube, *l*, are large pouches; this has forced its way toward the actinostome from the main water pouch; the tubes adjoining the lateral tubes are the shorter, *ch''* (diacœliac).
11. Cœliac view of embryo nearly in same stage of development.
12. Seen from the abactinal pole; *l*, lateral tubes.
13. The lateral tubes extend nearly to the actinostome; the locomotive flappers and accompanying chymiferous tubes, *ch'*, *ch''*, have become much lengthened and better separated (cœliac view).
14. Fig. 13, seen from the abactinal pole.
15. About in stage of fig. 13, seen from the diacœliac axis.
16. The chymiferous tubes are still more elongated than in the preceding stages (diacœliac view).
17. Cœliac view of embryo about in stage of fig. 16; the upper part of the chymiferous pouch has become a broad tube leading to the separate branches extending below the rows of locomotive flappers.
18. Embryo about in stage of fig 17, seen from the abactinal pole.
19. Two of the chymiferous tubes, *ch'*, have pushed their way to the actinostome (diacœliac view).
20. The edges of the cœliac apparatus have become fringed, from being mere simple lappets covering the opening leading into the chymiferous pouch; two of the chymiferous tubes, *ch'*, have united with the lateral tubes forming a ring round the actinal opening (cœliac view).
21. The shorter chymiferous tubes have nearly reached the circular actinal tube; the short processes in the chymiferous tubes, noticed in fig. 20, have become more prominent and are the first traces of the complicated system of branches forming the ovaries and spermaries in the adult (see fig. 24).
22. The short chymiferous tubes *ch''* have now united to the actinal ring thus completing the circuit of the chymiferous system. The branches of the tubes send out processes and the young *Idyia* differs now only quantitatively from the adult.
23. View from abactinal pole of *Idyia* (figs. 23-27, copied from Agassiz Contrib.)  $\frac{1}{2}$  n. s.

\*It is usually in the condition figured in the beginning of the Plate, figs. 1-8, that the young *Idyia* escapes from the egg case.

24. *Idyia* seen in profile to show ramifications of chymiferous systems and connection of chymiferous tubes with the lateral tubes,  $\frac{1}{2}$  n. s.

*Pleurobrachia rhododactyla.*

25. Profile of *Pleurobrachia rhododactyla*, natural size.  
25'. Somewhat magnified, seen from the abactinal pole.

*Bolina alata.*

26. *Bolina* seen from the broad side, n. s.  
27. *Bolina* seen from the abactinal pole, n. s.

## PLATE IV.

*Pleurobrachia rhododactyla.*

1. Fecundated egg of *Pleurobrachia*, 0.85<sup>mm</sup> in diam.
2. Thickening of the germinal layer at one pole.
3. Still greater thickening with corresponding depression in yolk mass.
4. Seen facing one of the protuberances forming the first traces of segmentation.
5. Dumb-bell state immediately preceding segmentation into four, seen obliquely.
6. One of the dumb-bells seen endwise.
7. Commencement of segmentation into eight masses.
8. Dumb-bell state of segmentation into eight, seen from actinal side.
9. Segmentation into eight masses completed.
10. Second segmentation of the small actinal spheres, already well advanced.
- 11-15. Different views showing increase of the small actinal spheres.
- 16-17. The small actinal spheres have greatly increased in number.
18. End view of an embryo somewhat older than fig. 11.
- 19, 20, 21. The small actinal spheres commence to encroach and cover the large yolk masses; fig. 19, seen from actinal side; 20 from the broad side; 21 from the side of the actinal trench.
22. Somewhat more advanced, seen at right angles to actinal trench.
23. About in stage of fig. 22; seen facing actinal trench.
24. The actinal spheres have encroached somewhat more upon the inner yolk masses.
25. About in stage of fig. 24; seen from actinal pole.
26. Seen from the abactinal pole.
27. Seen in profile.
28. Large yolk masses somewhat more broken up than preceding stages; seen from abactinal pole.
29. Seen in profile; yolk masses nearly entirely covered.
30. The actinal depression is unusually well marked far beyond its usual condition at this stage.
- 31-33. Various views of segmentation of the mulberry stage when actinal spheres have almost completely covered the inner yolk masses previous to the formation of a distinct wall as in fig. 34.
34. First trace of otolithic sac and of actinal depression.
35. About the same stage; seen from abactinal side.
36. Somewhat more advanced than fig. 34.
37. Digestive cavity well formed, walls thickened to form base of locomotive flappers.
38. Different embryo somewhat more advanced in some respects than fig. 37.
39. Digestive cavity of this embryo far advanced, but sensitive bulb and flappers retarded.
40. About in stage of fig. 31; seen from the actinal side.
41. The digestive cavity is gradually forcing its way towards the abactinal pole.
42. Somewhat more advanced seen from the actinal side.
43. About in stage of fig. 42 seen in profile; *v*, the base of locomotive flappers quite prominent; *t*, tentacular bulb.
44. Seen from the abactinal side about in stage of fig. 42.
45. Profile of embryo somewhat more advanced than fig. 43; the sensitive bulb and tentacular bulb have become quite prominent.

## PLATE V.

*Pleurobrachia rhododactyla.*

1. Pear-shaped embryo with four otolites at base of sensitive bulb. Lettering as on Plates of *Idyia* with addition of *t* for tentacle.
2. Somewhat more advanced with band for locomotive flappers.
3. About in stage of fig. 2; seen from the abactinal pole.
4. About in same stage, seen from the actinal pole.
5. Locomotive flappers are developed as double rows of stiff bristles; first trace of chymiferous cavity as diverticulum of the digestive cavity.
6. Somewhat more advanced than fig. 5. The inner yolk masses of *Pleurobrachia* are early reduced to a small bulk owing to the great size of the digestive cavity, and of the tentacular bulbs which have been formed at their expense.
7. Same seen from the abactinal pole.
8. Somewhat older; otolites have formed a cluster of four within the sensitive bulb.
- 9, 10. The tentacular bulb now forms quite a marked handle to the outline of the young *Pleurobrachia*. The walls of the digestive cavity become comparatively thinner.
11. The gelatinous connecting tissue commences to form at base of the digestive cavity, between the outer wall and the actinal part of the large, inner yolk masses.
12. Same stage as fig. 11, seen from the abactinal pole.
13. Same seen from the actinal pole.
- 14-18. Different stages (at right angles to tentacular axis) showing the gradual concentration of the tentacular bulb, the lengthening of the tentacle, the diminution of the inner yolk masses, with the increase of the connecting tissue and the enlargement of the digestive cavity, the formation of the chymiferous pouch.
- 19, 20. The walls of the digestive cavity have become comparatively flexible, the inner yolk masses are reduced to a small cluster round the chymiferous pouch. The large cells of the connecting tissue are very prominent, running mainly at right angles to the vertical axis.
21. What is left of the yolk masses is placed above the level of the opening of the digestive cavity into the chymiferous pouch.
22. About in stage of fig. 21 seen facing the tentacular bulb.
23. The connecting gelatinous tissue has also formed at the abactinal pole and isolated the upper portion of the chymiferous pouch, as a short funnel.
24. The digestive cavity is quite flattened, the chymiferous pouch is a large rectangular cavity lined with powerful vibratile cilia, but not having as yet very distinct walls.
25. The chymiferous pouch has become a still larger, rectangular cavity, with very mobile walls and a distinct opening connecting with the digestive cavity.
26. Another embryo nearly in same stage as fig. 25.
27. In nearly same stage (fig. 26) seen facing the tentacular bulb.
28. About same stage seen from the actinal pole. In this stage 21-28 the young *Pleurobrachia* usually escapes from the egg case.
29. Somewhat more advanced than fig. 27.
- 29a. Shows the mode of formation of the chymiferous tubes as pouches from the main chymiferous cavity.
30. Young *Pleurobrachia* somewhat more advanced than fig. 29 seen facing the tentacles.
31. Part of chymiferous tube, *ch*, of adult *Pleurobrachia*, showing position of spermaries, *s*, and of eggs *e*; *p*, basal plate of locomotive flapper.
32. Section of fig. 31; same lettering.



