

No. 4. — *Cristatella: the Origin and Development of the Individual in the Colony.* By C. B. DAVENPORT.¹

CONTENTS.

	Page		Page
I. Introduction	101	5. Origin of the Central Nervous System	127
II. Architecture of the Colony	103	6. Origin of the Funiculus and Muscles	128
III. Origin of the Individual	106	IV. Organogeny.—Development of	
A. Observations.—Origin of		1. The Ring Canal	129
1. The Bud	107	2. The Lophophore	130
2. The Alimentary Tract	111	3. The Tentacles	135
3. The Central Nervous System	113	4. The Lophophoric Nerves	136
4. The Kamptoderm	115	5. The Epistome	138
5. The Funiculus and Muscles	115	6. The Alimentary Tract	139
6. The Body-wall	117	7. The Funiculus and Muscles	141
7. The Radial Partitions	119	8. Origin and Development of the Parietovaginal Muscles	143
B. Comparative and Theoretical Review of the Observations on the Origin of the Individual	120	9. Disintegration of the Neck of the Polypide	144
1. Origin of the Polypide	121	10. Development of the Body-wall	144
2. Interrelation of the Individuals in the Colony	121	Summary	145
3. Origin of the Layers	123	Bibliography	148
4. Origin of the Alimentary Tract	127	Explanation of Figures	152

I. Introduction.

At the suggestion of Dr. E. L. Mark, I began, in the spring of 1889, the study of fresh-water Bryozoa. While at the Laboratory of the United States Fish Commission, at Woods Holl, Mass., where, through the kindness of Mr. A. Agassiz, I had the opportunity of spending the

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following summer, I gathered most of the material for this study. I found an excellent place for collection in Fresh Pond, Falmouth, where *Fredericella* and *Plumatella* were also gathered. Upon my first visit to this pond (July 5th), I found at its outlet *Cristatella* exceedingly abundant on the leaves of the pond-lilies. A month later, the same locality yielded very few specimens; but about September 5th I found them plentiful again, and at the same time noticed the phenomenon described by Kraepelin and by Braem, — that some of the statoblasts of *Plumatella* had already hatched. Colonies of from five to twenty individuals were observed with the two halves of the statoblast still adhering to their bases. A few colonies of *Cristatella* were also gathered in the latter part of August from Trinity Lake, New York.

The material collected was killed with a variety of reagents. Cold corrosive sublimate gave the best results. In staining, I always found Czoker's cochineal the most satisfactory dye for the study of the embryonic cells of the bud.

As Haddon ('83, pp. 539-546) has reviewed the most important part of the bibliography of budding in *Phylactolæmata* which had been published at the time of his writing, I shall be relieved from giving here any extended historical account of the earlier researches. The contributions of Nitsche ('75) and Hatschek ('77) are well known. Reinhard has published a preliminary article ('80^a, '80^b) on this subject in the *Zoologischer Anzeiger*; but his two more important papers ('82 and '88) I have unfortunately not seen. Braem's ('88, '89^a, and '89^b) three preliminary papers concerning budding in fresh-water Bryozoa correct some erroneous statements of Nitsche, and support Hatschek's view of the origin of the polypide. The results at which I have arrived concerning this last problem are similar to those of Braem, but his work has apparently been done chiefly on *Alcyonella*, mine on *Cristatella*. Finally, I believe there will be found in this paper something new on the organogeny, which Braem does not seem to have especially studied, and which may be of general morphological importance. For these reasons, it has seemed to me desirable that I should publish my observations and conclusions, and I am the more inclined to do so because our views are not in all points the same.

In the matter of nomenclature, my studies have not led me to a final conclusion as to the homologies of the axes of the individual, and therefore I fall back by preference on non-committal terms. The individual is bilaterally symmetrical. Parts nearer the mouth end of a line joining mouth and anus (i. e. nearer the margin of the colony) will be desig-

nated "anterior" or "oral"; parts nearer the anal end, "posterior" or "anal." To parts nearer the roof of the colony will be applied the term "superior," or "tectal"; to those nearer the sole, "inferior." Parts situated at either side of the sagittal plane of the individual are "lateral," and either right or left,—the individual facing the margin of the colony. In naming organs, I have preferably used the terms employed by Kraepelin ('87). I adopt the term polypide simply because it is a convenient name for a number of organs closely united anatomically, and arising from a common source embryologically.

II. Architecture of the Colony.

The colony of *Cristatella*, as is well known, consists of a closed sac, which is greatly elongated in old specimens, and has a flattened base or "sole," and a convex roof. The wall of this sac is known as the wall of the colony or cystiderm (Kraepelin). Suspended from the dorsal wall, and hanging in the common cavity of the colony, which may be called the *cœnocœl*, are to be seen numerous polypides in different stages of development. A more careful observation shows that the polypides lying nearest the median plane of the colony are the largest and oldest, those nearest the margin, conversely, smallest and youngest (Plate I. Fig. 1). All young colonies of *Cristatella* have been derived from one of two sources, eggs or statoblasts. According to Nitsche ('72, p. 469, Fig. 1), there are two polypides of the same age first developed in the cystid, which is a product of a fertilized ovum, and regarding these he fully agrees with Metschnikoff's ('71, p. 508) statement, "Die beiden Zooiden entwickeln sich wie gewöhnliche Knospen."

Nitsche ('75, pp. 351, 352) observed that in *Alcyonella* the primary polypides are placed with their oral sides turned from each other, and that the younger buds arise in the prolongation of the sagittal plane of the older polypides, and from that part of the cystid lying between the œsophagus of the older buds and the margin of the colony.

As Braem ('89, pp. 676–678) has shown, there is but one primary bud in the statoblast embryo. The younger buds formed in the statoblast arise on the oral side of the primary bud.

In *Cristatella*, says Braem ('88, p. 508), the newly hatched statoblast embryo already exhibits to the right and left of the adult primary polypide two nearly complete daughter individuals of unlike age, which are generally followed by two other sisters in the same relative positions, and a fifth in the median plane,—oral with respect to the

mother bud. These buds may produce new ones until the whole colony has attained the size of a pea; then young buds arise anawards of the primary polypide, and as the margin of the colony is protruded on each side of this point, the colony becomes heart-shaped. The two upper lobes of the heart are regions of great reproductive activity; they separate from each other, and thus transform the heart-shaped colony into an elongated one. Through the heaping together of buds effected by this process, a misproportion between the area (Flächenraum) and the circumference of the colony results, and the buds, which lie in longitudinal rows, soon come to be crowded. After this, they each give rise to only two daughter buds, a lateral and a younger median one.

To these observations of Braem I have little to add. I have figured (Plate X. Fig. 88) a young colony of *Cristatella*, containing about thirty polypides. This was taken in the latter part of July, and is probably an egg colony. My reasons for thinking so are, that the statoblasts of the preceding year form colonies in the early spring; that statoblasts of any year have never been seen, like those of *Alcyonella*, to hatch in the fall; and that there are, occupying the centre, two polypides of very nearly equal size and development, and probably therefore of nearly equal age. Surrounding these are eight younger individuals, nearly equal to each other in size, and these are in turn followed by two generations, of thirteen and seven individuals respectively, — the last generation evidently being as yet incomplete.

As Kraepelin ('87, pp. 38, 139, 167) clearly states, the *Cristatella* colony is comparable with those of *Pectinatella*, *Plumatella*, etc., and may be derived from them by imagining a condensation of those branching colonies. The radial partitions seen in Figure 88, *di sep. r.*, Plate X., are thus homologous with the lateral walls of the branches of a *Plumatella* colony; and just as in the latter, so here young individuals arise near the tips of the branches, and the older individuals degenerate. As in *Plumatella*, young individuals are produced not only distad of older, but also laterad, thus founding new branches, so in *Cristatella* we find young buds having the same positions. These facts will be better appreciated by a reference to Figure 1, which shows a portion of the margin of a mature colony. It is here clearly seen, (1) that, as has long been known, the youngest individuals are placed nearest to the margin, and that therefore, as one passes towards the centre, one encounters successively older and older individuals; and (2) that, as Kraepelin ('87, Fig. 134) has already figured, the older individuals are arranged in a quincunx fashion.

The bit of the margin figured may be regarded as typical, not only on account of its symmetry, but also because of the fact that the youngest individuals are placed at the normal distance from the margin. Although I have seen these conditions

repeated in enough instances to assure me of their normal nature, yet, owing to a crowding of polypides, both among themselves and to the margin of the colony, and also to the consequent displacement of polypides, the appearances which I am about to describe are often obscured.

First, the interrelations of the individuals included within compartments 1-8 are exactly repeated in compartments 9-16. The same repetition holds true for the remainder of this side of the colony. On the opposite side, the number varies from six to eight. At the ends of the colony, owing to crowding of individuals, it is difficult to count with accuracy. Since all individuals are derived from preceding ones, the conclusion seems reasonable that the inhabitants of these eight branches were derived from a common ancestor. It is interesting that from each of these ancestors the same number of branches and an almost equal number of individuals are produced, and that the corresponding individuals in each of these families, e. g. Figure A, 4, 5 and 12, 13, and 7, 8 and 15, 16, are similar in

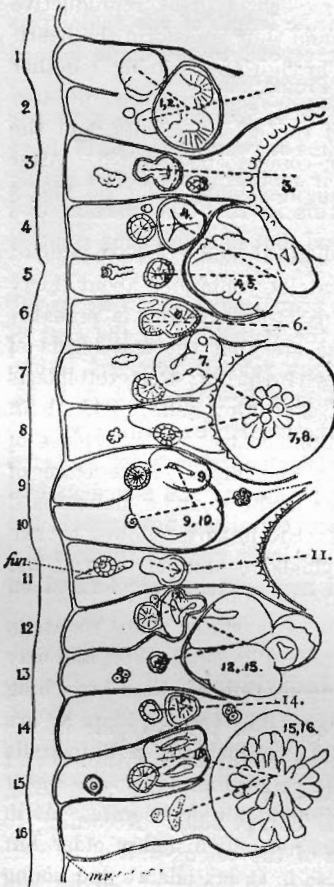


FIGURE A.

position, and of the same stage of development.

Secondly, most individuals figured have given rise to two individuals; some, on the contrary, to but one. Of the two individuals produced, one (the older) passes into a second (new) compartment, and so forms a new branch. The younger, however, remains in the ancestral compartment, and thus continues the ancestral branch. See, e. g., individual

4, 5, of Figure A. The buds which give rise to new compartments may be called lateral buds, in accordance with Braem's terminology; those which prolong the ancestral branch, median buds. Where only one individual arises, it is a median bud. These conclusions regarding the relationship of buds are based solely upon the length of the radial partitions, the inner extremities of which correspond to the angle formed by two branches in branching genera like *Plumatella*.

Thirdly, while the lateral buds, Figure A, 4, 5, and 12, 13, give rise directly to new buds, median buds of the same or younger age, 6, 14, have moved to a considerable distance from their mother buds before giving rise to new individuals. The effect of this is, that the median bud comes to lie, not alongside of the lateral bud, but in a quincunx position relatively to it.

Fourthly, lateral buds (branches) may arise from either side of the budding individual. Although most of the branching in the part of the colony figured in the cut is to the right, yet the youngest lateral buds are being given off to the left. So in compartments 4, 6, 7, 12, the funiculus indicating the point where the median bud will arise.

To recapitulate: The descendants of common ancestors are arranged similarly in the same region of the colony; a lateral and a median bud may arise from a single individual, the first forming a new branch, the latter continuing the ancestral one; median buds migrate towards the margin before producing new buds; and new branches are formed on either side of the ancestral branches.

III. Origin of the Individual.

Two essentially different views of the origin of the polypide in the adult colony of *Phylactolæmata* have been maintained within recent years. The first is that advanced by Nitsche ('75, pp. 349, 352, 353), and adopted by Reinhard¹ ('80^a, p. 211, '80^b, p. 235). According to these authors, the outer of the two layers of the colony-wall gives rise, either by a typical or a potential invagination, to the inner cell layer of the bud,—the layer from which the lining of the alimentary tract and the nervous system both arise,—and pushes before it the inner layer

¹ Reinhard says in his preliminary article, "Meiner Meinung nach entwickelt sich die Knospe in Folge einer Verdickung des Ectoderms, in welche dann die Zellen des Entoderms eindringen," but Brandt's abstract of the paper read by Reinhard before the Zoological Section of the Russian Association, places entoderm for ectoderm, and *vice versa*,—a rendering more in accordance with Reinhard's statements in the context.

of the colony-wall, which thus becomes the outer layer of the bud. Hence the buds arise independently of each other.

The second view is that advanced by Hatschek ('77, pp. 538, 539, Fig. 3). He asserted that in *Cristatella* "Die Schichten der jüngeren Knospe stammen von denen der nächst älteren direct ab." Finally, Braem ('88, p. 505) agrees essentially with Hatschek, and believes that a typical double bud, although it does not always appear, is the fundamental condition. His preliminary account clearly shows that precisely the same condition of affairs, except in so far as modified by the less metamorphosed condition of the ectoderm, exists in *Alcyonella* as in *Cristatella*.

A. OBSERVATIONS.

1. *Origin of the Bud.* — The result of my own work has been to lead me to a conclusion differing from both of these two views, but more like the second than the first. By my view, as well as by Braem's, Nitsche's two types of single and "double" buds are united into one. I would not say, with Hatschek, that the two layers of the younger bud arise directly from those of the next older, but that each of the corresponding layers of the younger and next older buds arises from the same mass of indifferent embryonic tissue. In some cases, each of the layers of the daughter polypide does arise from the corresponding layers of the very young mother bud. In other cases each of the two layers out of which the two layers of the older bud were constructed contributes cells to form the corresponding layers of the younger bud, but the cells thus contributed have never formed any essential part of the older bud. All gradations between these two types occur. For convenience' sake, we may always call the older polypide the mother; the younger polypide, the daughter. Figure 3 (Plate I.) shows a well advanced bud (Stage VIII.) which consists of two layers of cells, an inner, *i.*, composed of a high columnar epithelium arranged about a narrow lumen; and an outer, *ex.*, of more cubical cells. In a region (I) on the bud which is near the attachment of its oral face to the body-wall there is a marked evagination of the contour, caused in part by a thickening of the outer layer, and in part by a slight increase in the diameter of the inner. This thickening of the wall is the first indication of the formation of a younger bud, which is to arise at this place. Figures 22, II., 16, VI. (Plate III.), and 11, VI. (Plate II.) show later stages of buds originating in the same manner as that of Figure 3. The mother bud has grown larger, as has also its lumen. The outline in its upper oral region has become much folded as

a result of cell proliferation, and a deep pocket has been formed lined by a layer of cells which are still a part of the inner layer of the mother bud. The outer layer of the latter has also been protruded by the activity of the inner layer, and its cells go to form the outer layer of the young bud. Still another point is to be observed. The centre of the young bud has moved away from the centre of the neck of the mother bud, and thus the former lies nearer to the margin of the colony than the latter. Figure 17, VII. (Plate III.) shows a still more advanced stage in the development of the bud, in which it is sharply separated from its parent, but its inner and its outer layers are still in direct continuity with the inner and outer layers respectively of the mother.

I have selected this series from the many which might have been chosen to show the origin of the polypide, because it is an intermediate type between two extremes, and because by it the other cases receive an easy explanation. All cases of budding, however, seem to conform to this general law: the greater the difference in age between the youngest and the next older bud, the greater the distance between the points at which they begin to develop. Thus the typical case of a "double bud" is that in which two buds appear to arise at the same time. They originate, as Nitsche observed, from a common mass of cells. A case of two buds, one only slightly younger than the other, is seen in Figure 5. By comparing with Figure 3, in which the older polypide is older than VII., Figure 5, the difference between the younger buds will be apparent. On the other hand, Figure 4 illustrates a comparatively late formation of the younger bud. The older bud had attained a stage corresponding to Figure 18 (Plate III.), but the younger bud is not older than that seen in Figure 22, II. Just as in the latter case the two layers of the older bud went respectively into those of the younger, so in the present case a direct continuity can be traced between the cells of the inner and outer layers respectively of the younger and older buds. The evidence that the cells composing the inner layer of the young bud have not arisen directly from the ectoderm is derived not only from the continuity of both cell layers of the two buds, but from the presence of the apparently unmodified ectodermic cells lying above the inner layer of the young bud, and sharply marked off from it. Figure 6 shows a later stage of this same type, in which the layers of the young bud are seen well formed, but still very sharply separated from the overlying ectodermal cells. These series afford an interpretation of the extreme type of budding shown in Figure 2, which is not uncommon. The mother polypide has reached a stage corresponding to Figure 18, Plate III. To the left of the neck of

the polypide and towards the margin is the funiculus, *fun.* Between it and the neck of the polypide the cœlomic epithelium is thickened and its cell boundaries have become evident. Directly above this region, and immediately above the muscularis, is a row of cells, which stain deeply and show other evidences of being embryonic. These are directly continuous with the neck cells of the older polypide, exactly as was the case with the cells of the inner layer in Figures 4 and 6 (Plate I.). In fact, they are in every way comparable with these. Figures 8 and 9 (Plate II.) show slightly later stages. The funiculus has moved farther from the parent bud, the future outer layer (*ex.*) has become thicker, and its cells are columnar and sharply marked off from each other. The inner layer (*i.*) of the new individual is represented by a thicker, stolon-like mass of cells, which is in direct continuation with the inner layer of the mother bud, from which it was doubtless derived.

A stage which, on account of the greater distance of the funiculus from the older polypide, I believe to be slightly more advanced than Figure 8, is shown in Figure 9. In the section drawn, the inner cell mass (*i.*) exhibits few nuclei, but they are more numerous in adjacent sections. The band of protoplasm connecting this young bud with the mother is perceptibly smaller than in the preceding stage. The cells of the inner layer form a mass sharply marked off from the ectoderm; those of the outer layer are greatly thickened, as in the last stage.

A peculiar thickening of what I regard as Nitsche's "Stützlamele" takes place between the young bud and the mother polypide. This is shown in Figures 9 and 10 at *mu.* It is not stained by Czoker's cochineal, and the circular muscle fibres, here cut transversely, are very conspicuous in the midst of it. As I have noticed this appearance only in the cases of young buds which have originated like those of Figures 9 and 10, and of others of about their age, (and it is in these buds and at this age that migration from the older polypides takes place,) I believe that there is some connection between this condition of the muscularis and the disturbance which such a migration must cause.

I have already (page 106) referred to the fact that in some cases median buds are found far removed from the mother polypide, although in an early stage of development. Stage IV. is the youngest in which such buds have been found.

The cells of the mass destined to form the inner layer of the bud multiply rapidly after they have reached a proper position, and there is considerable protrusion of the cœlomic epithelium into the body cavity. The fact, that during its extensive migration the bud increased only

slightly, whereas it now begins to develop rapidly, leads to the presumption that it has ceased to migrate, and has come to a state of comparative rest, relative to the surrounding ectodermal cells.

One of the first indications of further development is seen in the arrangement of the cells of the inner layer, which is such that their nuclei come to lie near the surface of a hemisphere whose convex side is turned toward the cœnocœl. The beginning of this process is seen in Figure 10 (Plate II.), and, further progressed, in Figure 11. Figure 14 exhibits a still later stage in the development of the polypide. In the lower portion of the two-layered sac of this figure a separation of the cells (*lu. gm.*) has begun. This is the first indication of the atrium.

In all cases there exists at this stage a condition of the ectoderm like that shown in Figures 5 and 14. The absence of ectodermal cells directly over the bud may be accounted for by supposing that they have come to lie upon, and form part of, the neck of the polypide. While it would be impossible to deny that they *might* migrate through the cells composing the neck of the polypide, and thus come to form the nervous elements, a careful study of the successive stages figured will not show the slightest evidence of any such migration, nor is it *a priori* probable, from what is known of the action of epithelium the world over, that such a migration would occur.¹

According to the description of Nitsche ('75, p. 353), there is a lumen in the bud of *Alcyonella* (where the ectoderm is much less metamorphosed than in *Cristatella*), which is always in direct communication with the outer world, the bud having been formed by a typical invagination. Braem ('88, pp. 506, 507), however, states that he has never seen in *Alcyonella* this communication of the bud cavity with the outer world. In the much more obscure process of polypide development in *Gymnolæmata* the lumen first appears after the cells of that mass from which the bud is to arise have arranged themselves in two concentric layers. In *Endoprocta*, according to Nitsche ('75, p. 374) and Seeliger ('89, p. 179), the lumen arises by a virtual or actual invagi-

¹ Since writing the above paragraph I have cut some sections of *Plumatella* in which this process is much clearer, owing to the absence of secreted bodies in the ectoderm. Instead of a few ectodermal cells dropping down upon the upper part of the neck of the polypide, as is the case in *Cristatella*, there is a cup-shaped invagination of the ectoderm, which is quite deep, and thus gives rise to an elongated "neck." That none of these ectodermal cells go to form any part of the polypide proper is certain in *Plumatella*. But it is also true, that ectodermal cells are thus incorporated into the neck of the polypide, and probably into the stolon which proceeds from it.

nation and remains always in communication with the surrounding medium. In *Cristatella* the lumen is formed in the bud at the time when its diameter perpendicular to the roof of the colony slightly exceeds that parallel to it. As Figure 14 (Plate II.) shows, this cavity (*lu. gm.*) first makes its appearance in the distal part of the central mass of cells. There are always cells lying above the lumen, and thus cutting off the ectoderm from contact with it. The two layers from which, according to my view, all of the cells of the adult polypide are derived, are now completely established; and the cavity has already appeared which, by enlargement, out-pocketing, and the concrescence of its walls, gives rise to the atrium, and the lumina of the alimentary tract and supra-oesophageal ganglion.

The bud elongates, and often at this time, preparatory to giving rise to a new bud from its upper marginal angle, becomes bent or curved, the concavity always being next the daughter bud (see Figs. 3, 5, 11, and 22). By this change in form the bud becomes bilaterally symmetrical.

2. *Origin of the Alimentary Tract.* — The first organ derived from the two-layered sac is the alimentary tract. Nitsche ('75, p. 356) described the process of its formation in a very clear manner; but I believe he is in error. The original lumen of the bud represents, he says, the atrium and the lumen of the alimentary tract. The part lying nearest the attached end of the bud gives rise to the former; the latter is derived from the lower part of the lumen. These two regions become separated by the invagination of the two layers of the bud along a furrow on each side of the bud; just as though the walls of a two-layered hollow rubber ball were pressed together by a finger of each hand acting at opposite sides until the points of the fingers should be separated by the four layers of the ball only. By this process, mouth, anus, and the entire gut, would of course be formed at one time. Reinhard ('80^a, p. 212) appears to agree with Nitsche as to the method of origin of the alimentary tract. Braem ('89^b, pp. 677, 678) describes and figures diagrammatically this process in the statoblast of *Cristatella*. In the median plane of the bud there is an out-pocketing from the anal side of the atrium which involves both layers of the bud; it assumes the form of a comma, its blind end curving forward to meet the blind end of a lesser evagination of the oral part of the atrium, — the oesophagus. The blind ends of these two pockets meet, and by the breaking through of the intervening tissue their lumina freely communicate with each other, thus completing the alimentary tract. He adds: "Auch bei den Polypiden der fertigen Colonie der Darm durch Verwachsung eines analen

und eines später auftretenden oralen Schlauches, an deren Bildung freilich das äussere Knospenblatt nur secundär sich betheiligt, zu Stande kommt."

My own observations are nearly in accord with the statements of Braem, as opposed to Nitsche's. The older bud of Figure 11 (Plate II.) shows the first indication of the lumen of the posterior part of the alimentary tract near the attached portion of the bud. The cells of the inner layer are multiplying, and the lumen of the bud is broader here than elsewhere. The position of a daughter bud, VI. (on the oral side of the one under consideration), sufficiently indicates that the point marked *rt.* is in the region of the future anal opening. Figures 12 and 13 (Plate II.) show further stages in this same process. The lumen of the intestine is formed, not by constricting off a part of the original lumen of the bud, but by the rearrangement of cells at the progressing blind end of the pocket, which gradually moves towards the distal part of the larger or bud cavity. It is important to establish the fact that the alimentary tract is formed in the inner layer of the bud, and that its cells alone line the digestive cavity. Figures 20 and 21 (Plate III.) represent two successive sections out of five which pass through the inner layer; namely, the second and the third counting from the attached to the free end of the bud. The sections were cut at right angles to the plane of Figure 11 nearly along the lines 20 and 21 respectively. It will be seen that the inner layer alone is implicated in the lining of the alimentary pocket at this early age. They also show clearly the incorrectness of the statements of Nitsche on this point. Figures 24, 25, and 26 (Plate IV.) are three sections cut through a bud of about the age of that represented in Figure 13 (Plate II.), and at right angles to the plane of the latter, and in the direction of the lines 24, 25, and 26 respectively. A section cut beyond the end of the intestine, in Figure 13, is not represented. It shows that the lumen of the alimentary tract is absent at this plane. A comparison of Figures 20 (Plate III.) and 26 (Plate IV.) shows that the lumen of the bud, *lu. gm.* (which we may call the atrium from its resemblance to a space having the same relations in Entoprocta), has increased in volume owing to a growth of the lateral walls. On account of the more rapid elongation of the anal than of the oral side, the axis of the alimentary tract comes to take a horizontal position, as shown in Figures 17 and 18, Plate III. (Compare also Figs. 27-29, Plate IV.) The blind end of the digestive sac comes very close to the blind end of another pocket formed on the oral side, the œsophagus, and soon the two communicate directly. At the same time, the inner cell-layer of the

middle portion of the alimentary tract has been quite cut off from that of the atrium by a constriction, the beginning of which is seen at *ex.*, Figure 24 (Plate IV.) and in a later stage at *ex.*, Figure 28. The cells of the outer layer are next pushed into the place of constriction and remove the alimentary tract at this point still further from the atrium, as is shown in Figures 18 (Plate III.) and 28, *ex.* (Plate IV.). The error of Nitsche is explainable on the ground that he believed the stage of Figure 18 to be the earliest in the development of the alimentary tract.

3. *Origin of the Central Nervous System.* — Metschnikoff ('71, p. 508) first clearly recognized that the supra-oesophageal ganglion of *Phylactolæmata* is derived from the inner cell-layer of the bud, — the same layer which gives rise to the inner lining of the alimentary tract. Nitsche ('75, pp. 359, 360) described and figured in an insufficient and not wholly accurate way the process of the formation of this organ. According to my observations, the central nervous system arises directly over the middle of the horizontally placed alimentary tract in the position marked *gn.* in Figure 18, Plate III. (compare also Figs. 17 and 28, *pam. gn.*). The process by which the ganglion with its internal cavity (Plate VIII. Fig. 73, *lu. gn.*) is formed will be more easily understood if the reading of the text be accompanied by reference to the following sections. Figures 17, 18, 19, Plate III., and Figure 73, Plate VIII., show successive stages in sagittal section. Figures 27–29, Plate IV., from a single individual, are vertical right-and-left sections, the positions of which are indicated by the lines 27, 28, 29 of Figure 17. Figures 30–32 are similar sections from an older individual (see lines 30, 31, and 32, numbered at the lower border of Fig. 18), and Figures 33–38 are from a still older polypide (compare lines 33–38, Fig. 19). By a study of these sections, it is seen that the cells forming the floor of the brain, *pam. gn.*, are derived from the inner layer of the bud, and indeed from the very region of the layer which furnished cells to line the alimentary tract (Plate II. Fig. 13, Plate IV. Figs. 25 and 24, *ga.*), and therefore that the layer of cells forming the floor of the ganglion is directly continuous posteriorly through the anal opening (Plate II. Fig. 13, *an.*) with the wall of the rectum, and anteriorly with the lining of the oesophagus. The first marked differentiation of this region is effected by the sinking of the centre of the floor of the neural tract (Fig. 18, *gn.*), thus forming a shallow pit, which opens directly into the atrium above.

The *closure of the walls of the ganglion* above must now be considered. Concerning this process, Nitsche says: "Die Ränder dieser Einstülpung [my 'shallow pit'] wachsen nun wie die Ränder der Medullarrinne

eines Wirbelthierembryos gegen einander, und wie in letzterem Falle eine hohle Röhre von der dorsalen Leibeswand des Thieres abgeschnürt wird, so wird hier eine hohle *Blase* von der Wand des Polypids abgeschnürt. In unserem Falle ist aber die Wandung an der diese *Ab-schnürung* vor sich geht, zweischichtig." The two layers referred to were those of the median walls of a pair of invaginations of the latero-anal sides of the wall of the atrium, — the beginnings of the lophophoric arms (*br. loph.*, Figs. 37, 38, Plate IV., and Figs. 61, 62, Plate VII.).

The process of closure is in reality somewhat different from Nitsche's conception of it. The axes of the pockets which go to form the lophophoric arms are, at first, directed inward, upward, and slightly oralward (Plate I. Fig. 7, *br. loph.*). By means of these invaginations the cell layers lining the atrium on opposite sides are brought into contact at a point between the rectum and the ganglionic pit (Plate V. Fig. 43, *loph.'*). This approximation of the walls may, perhaps, better be said to be a continuation upward of the process by which the alimentary tract was cut off from the atrium (after the lumen of the former was formed), and by which cells of the outer layer of the bud came to intrude themselves between these two regions (Plate IV. Fig. 35, *ex.*); for the lateral furrows, by the formation of which this act is performed, are, on each side, continuous with the lophophoric pockets, and above end blindly in them. By the approximation and fusion of the inner layers of the atrium several things are accomplished. The posterior wall of the brain is formed (Plate IV. Fig. 39, *loph.'*), the anus is carried farther up (compare Plate III. Fig. 19, and Plate VIII. Fig. 73, *an.*), and by a continuation of the constricting process the cavities of the lophophore on opposite sides of the polypide are brought into communication between the ganglion and the rectum at a point opposite the letters *lu. gm.* in Figure 63 (Plate VII.), whereas they formerly communicated only outside the alimentary tract.

Oralward from the lophophoric pockets there is a thickening of the inner layer above the floor (*pam. gn.*) of the ganglion on each side (Plate IV. Figs. 28 and 31). Later, each of these thickenings becomes a fold involving the inner layer of the bud only (Plate IV. Fig. 35). The upper and lower halves of this pair of folds respectively fuse in the sagittal plane, the last point at which the union occurs being near the œsophagus (Plate III. Fig. 19). Anteriorly the rim of the shallow brain-pit rises up as a third fold, and the ganglion becomes a sac whose mouth is bounded by the edges of the folds, the advance of which causes it to become more and more constricted. These folds are the pair of folds

above the cavity of the ganglion, and the one between the cavity of the ganglion and the œsophagus. The outer layers of these three folds respectively fuse immediately behind the œsophagus; the inner layers are constricted off, but without closing the neck of the sac. Consequently the neck of the ganglionic sac, instead of opening into the atrium, now abuts upon the inner cell-layer at the angle between the floor of the atrium and the œsophagus. The lower layers of the horizontal folds thus become the upper wall of the ganglion (Fig. 35, *tot. gn.*); the upper layers form the new floor of the atrium (Fig. 73, *pam. atr.*), which lies between the lophophore arms, is continuous with its median walls, and passes over into the walls of the alimentary tract both in front and behind. The outer layer of the young bud only secondarily makes its way in between the upper and lower layers of these folds. It ultimately takes the form of a double layer embracing a space, which is the epistomic canal. (Plate VIII. Fig. 73, *lu. gn.*, Plate V. Fig. 52, *lu. gn., can. e. stm.*)

4. *Origin of the Kamptoderm.*— While the alimentary tract, lophophore arms, and nervous system are being marked out in the lower portion of the bud, these organs become farther removed from the wall of the colony by an enlargement of the atrium to meet the demands of the augmenting volume of the lophophore. *Pari passu* with this enlargement of the atrium, its walls diminish in thickness (compare *kmp. drm.*, Fig. 73, Plate VIII., with Fig. 18, Plate III.). This is rather the result of a failure of the cells to multiply in proportion as the area of the wall increases, than of a decrease in the number of cells already formed. Both the inner and outer cell-layers of the bud take part in the formation of this wall, as is evident from the figures. The wall of the atrium was called "tentacular sheath" by Allman ('56, p. 12) and Nitsche, but Kraepelin ('87, p. 19) employs the name "kamptoderm" for this structure. I prefer this term to "tentacular sheath," and have employed it both on account of the reasons given by him and because it may be easily inflected, whereas "tentacular sheath" may not. The kamptoderm, then, is formed of the upper portion of the bud, and both of its cell-layers are concerned in its formation and persist in the adult.

5. *Origin of the Funiculus and Muscles.*— Nitsche ('75, pp. 353, 354) did not see the origin of the *funiculus*, but states that it suddenly occurs lying close along the oral side of the bud, to which one end is attached. Its proximal end is fastened, he says, to the inner layer of the colony-wall, and by the growth of the latter between the funiculus and the neck of the bud this end retreats from the young polypide. Braem

('88, p. 533) asserts that the funiculus arises as a longitudinal ridge on the outer layer of the oral wall of the young polypide at the time of the formation of the alimentary tract, and that the cells of this ridge are cut off from the bud to form the funicular cord. Soon after this, embryonic cells from the inner layer of the young polypide penetrate into the midst of the cord through its proximal end, and thus lay the foundation of the statoblast.

Concerning the origin of the *muscles*, Nitsche ('75, p. 354) states that they are simple elements of the outer cell-layer of the bud, which were originally situated in the angle of attachment of the bud to the inner layer of the colony-wall, and that by the growth of this wall they become drawn out into spindle-shaped cells.

I have decided to treat of these two organs together, since their origin and development are curiously similar. According to my belief, both arise, in part at least, from the inner cell-layer of the colony-wall. At a stage slightly earlier than that of the first appearance of the fully formed funiculus (Plate II, Fig. 11, *cl. fun.*), I have always found a disturbed condition of the cœlomic epithelium. This is particularly noticeable on that side of the young lateral bud upon which the median bud is about to arise. In some cases I have seen the cells of this layer taking on all the characters of wandering cells, as seen at *cl. fun.*, Figure 22, Plate III., where some have already begun to group themselves into a funiculus-like cord. At Figure 57, *cl. fun.*, Plate VI., the funiculus is seen lying close to the oral wall of the polypide. That it has not arisen in precisely the manner described by Braem is probable from this figure alone, for the proximal end of the funiculus is not yet connected with the wall of the colony. If my view is correct, this connection arises only secondarily (Fig. 2, *fun.*). I am, however, inclined to believe that the distal end of the funiculus arises in a different way from the proximal, and in the manner described by Braem. My evidence for this is, that I have twice seen at this point cells in the act of dividing so as to contribute daughter cells to the funiculus. Figure 53, Plate VI., shows the condition of the distal end of the funiculus, *fun.*, which passes, without any line of demarcation, into the outer layer of the bud; this layer is normally one cell thick, but in the region of funicular formation it is two cells thick. The proximal end of the funiculus is, at this stage, attached to the cœlomic epithelium of the roof of the colony, *tot.* That an attachment should occur in this manner, and become quite intimate, is not strange, considering the origin of the funiculus from amœboid cells, and the fact that, even at a late

stage of development, this character is still retained by much of its tissue. (See, for example, Fig. 77, *fun.*, Plate IX.)

The great *retractor* and *rotator muscles* have, I believe, like the funiculus, a double origin. They arise from the outer layer of the bud, on the one hand, and from the cœlomic epithelium on the other. The first indication of the differentiation of the muscle cells consists in a disturbance in the upper lateral edge of the outer layer of the bud at about the stage of Figure 17, Plate III. This is shown in dorso-ventral sections through this region (*cl. mu.*, Figs. 24, 26, Plate IV.). Later, the disturbance becomes more marked, and cells having a semi-amœboid character appear to be proliferated (*cl. mu.*, Fig. 33, Plate IV.), and to migrate from the bud towards the cœlomic epithelium. During this process the cells of the latter layer also are active, and some of them, elongating, reach towards the young polypide, as seems to be clearly shown at *cl. mus.*, Figure 54, Plate VI. It is significant that, since each of the two upper lateral edges of the bud lies near a radial partition, the muscles also are always formed in close proximity to one (*di sep. r.*, Fig. 54, Plate VI.; Fig. 30, Plate IV.). It will thus be observed that, both in the case of the funiculus and of the muscles, the end which is attached to the wall of the colony arises at a point which is remote from that of its attachment to the adult. The migration to the later positions will be treated of farther on. (See page 141.)

6. *Origin of the Body-wall.* — As already shown (page 104), the body-wall of the individual of a *Cristatella* colony includes not only the endocyst of authors, — the roof and the sole, — but also the radial partitions.

Braem ('88, pp. 506, 507) concludes "dass die polypoide Knospenanlage . . . nicht allein das Polypid nebst den Tochterknospen liefert, sondern dass auch die zugehörigen Cystide aus ihr und zwar aus ihrem Halstheil entwickelt werden." I believe that a portion of the "cystid," or body-wall, is thus formed in *Cristatella*, but not the whole.

If one compares the relations of the polypide to its daughter bud in Figures 3 (Plate I.) and 17 (Plate III.), and reflects that later the daughter bud is to be found still farther from the mother bud, he is forced to one or the other of two conclusions: either the young bud is pushed from the mother by a proliferation of cells from the neck of the polypide without causing an increase in the length of the body-wall itself, or there is an actual increase in the length of the body-wall, produced either by the proliferation of cells already existing in it, or by the addition and subsequent proliferation of cells from the neck of the mother

polypide; and this increase in length, occurring between the polypide and bud, carries the two apart. Unfortunately, I am unable to state definitely how this migration of the young bud away from the mother is effected. If the ectoderm increases in length between the two buds by the proliferation of cells already existing in it, that fact ought to be evinced by a distorted condition of the old cell-walls of the highly metamorphosed cells of the ectoderm. For, since most of the active protoplasm is at the base of the ectoderm, its area will increase faster than will the area of the surface of the ectoderm; and the latter will either rupture or stretch, or else the ectoderm will become concave on its outer side. An application of these criteria to sections of the body-wall in the budding region leads to the conclusion that the ectoderm of *Cristatella* increases here very slightly, if at all, by a proliferation of cells already existing in it. A search for cell division in this region has yielded the same negative results. There can be no doubt that cells are added to the ectoderm from the neck of the polypide. The process takes place, however, after the daughter bud is well established at some distance from the mother bud. The proliferation of these cells ruptures the old cell-walls of the ectoderm, and increases the area of the body-wall. I shall have occasion to speak of this process more fully in treating of the later period to which it belongs.

There remains, then, the conclusion, that the cells which go to form the inner layer of the young bud are pushed from the neck of the next older bud by a proliferation of cells in the stolon-like mass, without causing an increase in the area of the body-wall itself. Moreover, I have seen cell proliferation in the stolon-like mass. Another series of facts will lead us to this same conclusion.

Though the body-wall does not increase by cell proliferation between buds, it does so, I believe, at the margin of the colony. This, it is true, cannot be directly observed with ease, since the multiplication of cells, which tends to increase the breadth of the colony, must also occur at the margin, and one cannot be certain what dimension of the colony wall will be augmented by any given case of nuclear division. My belief rests on the following evidence. (1) In the same adult colony the distance of the youngest bud from the margin is not the same in all regions. This is not what we should expect if the distance of the youngest polypides from the margin remained unchanged during the growth of the colony. (2) There is a gradual increase in the amount of metamorphosis exhibited by the cells as one passes from the margin towards the middle of the roof. Figure 60 (Plate VI.) shows a rather

marked example of a very common, although not universal, condition of the lateral margin of the colony. The epithelium of the margin is composed of columnar cells, which are higher (54μ) than those of the roof (48μ), and also of a less average diameter (8.4μ) than the latter (18.2μ). Moreover, the cells are very little metamorphosed. In passing towards the roof (*tct.*), the cells are seen to become more and more metamorphosed, the secreted bodies (*cp. sec.*) becoming relatively larger. Figure 55 represents the margin in a more metamorphosed state than Figure 60. Although this condition of things is not incompatible with the idea of a passive margin, it strongly suggests that this region is one of proliferation, by which cells are added to the roof, and thus the distance from the youngest polypide to the margin is virtually increased. This conclusion receives a very important confirmation from the study of the origin of the radial partitions, the treatment of which must be deferred for the moment. Although new cells are being added to the roof at the margin, yet the distance from the youngest polypide to the margin is not greater in old than in young colonies. How, then, is the approximate constancy of this distance maintained? Evidently it can only be by the process (which I have already shown must take place) of migration of some of the young buds at the base of the ectoderm, particularly in the case of median buds. The tendency of the migration of young buds towards the margin is to diminish the distance between the front of the budding region and the margin of the colony. The tendency of cell proliferation at the margin is to increase that distance. The actual distance is the resultant of these two opposing factors, and may be less or greater in different parts of the same colony, according as the one or the other is the more active. If we assume, further, that the cells added to the roof and sole from the margin plus those derived from the necks of the polypides are equal in amount to those lost by the degeneration of individuals in the middle of the colony, we have a sufficient explanation of the fact, observed long ago, that the adult colony of *Cristatella* maintains a nearly constant width.

7. *Origin of the Radial Partitions.* — I know of nothing on this subject by any previous author. The radial partitions consist of a muscularis covered on both faces by a very thin epithelial layer (Plate X. Fig. 95, 1). The muscle fibres of the muscularis arise from the already formed longitudinal muscles of the wall of the colony at the region of transition from the sole to the roof (Plate VI. Fig. 55, *mu.*). As the muscle fibres move into the cœnocœl, they carry before them the cœlo-

mic epithelium of the region from which they arise. It is owing to this method of origin that the epithelium comes to clothe both faces of the partition. The process by which the muscle fibres move into the cœnocœl appears to be this. The end of a fibre nearest the roof becomes fixed to a certain part of the muscularis of the roof, and is left behind with it when the margin is carried outward (potentially) as the result of cell proliferation. Thus from a nearly horizontal position the fibres attain a direction at first oblique, and then perpendicular to the sole. In some instances the upper ends of the fibres move through an arc of more than ninety degrees, so that they are ultimately directed upward and inward, i. e. towards the centre of the colony. (Compare *mu*, *mu'*, *mu''*, Fig. 55, Plate VI.). This process is also indicated in two horizontal sections (Plate X. Figs. 95 and 96), the former being nearer the sole than the latter. This is a region of active budding, and in consequence new compartments or *branches* are being rapidly formed. The numbers 3, 4, 5, and 6 (Figs. 95, 96) show the positions of young partitions, which are shorter above than below, owing to the oblique position assumed by the innermost muscle fibres of the partition. The oblique position is due to the fact already demonstrated (Fig. 55, Plate VI.), that the tectal end of the muscle of the partition first appears at the margin nearer the sole than the roof. At 2 (Fig. 96) there is apparently an interesting case of the formation of a new partition by the detachment of certain fibres from the muscularis of an old one. The fibres, moving away laterally, take with them a covering of cœlomic epithelium. Near the sole this process has progressed farther than it has nearer the roof, so that in Fig. 95 the detachment appears complete, whereas in Fig. 96 the union is still visible. This method of formation is intelligible when one considers that the muscularis of the partition often contains more than a single layer of muscle fibres. Thus, in Figure 87, *mu*., there are two or three layers of fibres in the section. Figure 86 represents a section cut vertically and at right angles to a partition near its union with the marginal wall of the colony, and shows three fibres of the longitudinal or inner layer of the muscularis lying side by side in the partition.

B. — COMPARATIVE AND THEORETICAL REVIEW OF THE OBSERVATIONS ON
THE ORIGIN OF THE INDIVIDUAL.

What bearing have the facts here adduced on those given for other groups of Bryozoa, and what is their probable significance in relation to the general problem of non-sexual reproduction?

1. *Origin of the Polypide.* — Lateral budding (as distinguished from linear budding, such as occurs in Turbellaria, Chaetopods, &c.) may be roughly classified under two types, in one of which the young individual arises *directly* from the body-wall of the parent, as in Hydra. In the other, the young arise, one after the other, from a mass of embryonic material derived from a parent individual, — from a stolon, as in Salpa. In the group of Bryozoa both of these methods seem to be present. In such a form as Paludicella (Allman, '56, pp. 35, 36, Korotneff, '75, p. 369) we have an example of the direct type; in Pedicellina we have a stoloniferous genus. Also in the marine Ectoprocta examples of both types appear to occur (e. g. Flustra, Hypophorella). To which of these classes does budding in Cristatella belong? It seems to me that we have here an instructive example of a transitional condition. The young polypide of Figure 3 arises directly from the mother polypide, and may represent a case of the first class. Is the type of Figure 2 a representative of the stoloniferous class? It seems to me that it partakes of the essentials of that class, although, as I have shown, it may be united by intermediate stages with the first class. I understand a stolon, in its morphological sense, to signify a mass of embryonic cells derived from a parent individual, and capable of reproducing non-sexually one or more daughter individuals at some distance from that parent. The condition shown in Figure 15, Plate II., in which the embryonic cells of the two layers represent the stolon, may fairly be said to answer to this definition. The mass of cells (III.) represents, then, the distal end of the stolon. But the stolon does not end here, although its further progress towards the margin is delayed. Not all of its cells go to form the polypide which arises at this place. On the contrary, some of them remain in the "neck" of the new polypide, in an indifferent histological condition, and later give rise, either directly, or by the intervention of a typical stolon, or by both, to one or two new buds. Those cells of the neck which do not thus pass over into new buds for the most part degenerate (page 144). According to this view, the neck of the polypide is to be regarded as at first essentially a portion of the stolon.

2. *Interrelation of the Individuals in the Colony.* — The interrelation of individuals in the colony in Cheilostomata has been most carefully investigated from a morphological standpoint by Nitsche ('71, pages 35, 36), who showed that, in opposition to Smitt's theory, each new individual arose from a single preceding one, and that the latter, in order to increase the breadth of the colony, might give rise to two individuals

instead of one. Reichert ('69, p. 311, Fig. 28, Plate VI.) has shown that in *Zoöbotryon* (one of the *Ctenostomata*) "an der Mantelfläche, und zwar einseitig, inseriren die Bryozoenköpfe mit Alternation in parallelen, wie es scheint, langgezogenen spiralig verlaufenden Reihen angeordnet." Nitsche ('75, p. 370) states that the buds in *Loxosoma* arise from the mother alternately on opposite sides, and that the younger the bud, the nearer it is to the foot of the parent individual.

Both Hatscheck ('77, pp. 517, 518, Fig. 33, Plate XXIX.) and Seeliger ('89, p. 176) show that in *Pedicellina* young individuals are developed in the plane of the older ones, and are successively formed at the growing tip of the stolon, towards which the oesophageal side of all individuals is turned. This relation is the same as that which we have found in *Cristatella*. In *Cheilostomata*, however, it is apparently the anus which is turned towards the budding margin.

Thus, throughout the group of *Bryozoa*, we find that the position which young buds assume in relation to older individuals is very definite.

I am inclined to believe that the radial partitions of *Cristatella* separate the morphological equivalents of the isolated branches of such a form as *Plumatella punctata* (see Kraepelin, '87, Taf. V. Figs. 124, 125). The type of budding which gives rise to the series of median buds may,



FIGURE B.

then, be represented, as seen from the side, by Figure B. The margin (*) will then represent that portion of the body-wall of the youngest individual, which will give rise to a part of the body-wall of the next younger individual.

The process by which the body-wall of the individual of *Cristatella* is formed is therefore, in my opinion, different from that which Braem describes in the case of *Alcyonella*, for he maintains that in *Alcyonella* the proper body-wall of an individual arises later than its polypide. In fact, the tip of the branch of *Alcyonella* is somewhat different from that of *Cristatella*. In the former, it is occupied by the polypide of a budding individual; in the latter, a part of the body-wall of the budding individual is pushed out beyond the polypide. In the former, the foundations of the daughter polypide are pushed out upon the body-wall of the mother, and begin to form their own proper body-wall; in the latter, the young bud migrates away into the modified part of the body-wall of the mother, which forms the extremity of the branch, and which now becomes a part of the body-wall of the daughter polypide. This distal part of the body-wall grows independently of the polypide by interstitial growth, and thus differs from any part of the body-wall

of the individual of *Alcyonella*, for all of it, according to Braem, is derived from the neck of its own polypide. This last method of origin of the body-wall I believe to be also present in *Cristatella*, as well as in *Alcyonella*, as I shall have occasion to show later (page 144).

In *Paludicella*, according to both Allman ('56, pp. 35, 36) and Korotneff ('75, p. 369), the formation of the body-wall of the new individual is begun before the appearance of the polypide. In Cheilostomata, as both Nitsche ('71, p. 22) and Vigelius ('84, p. 75) have shown, and in Ctenostomata, as demonstrated by Ehlers ('76, pp. 91, 92), the "zoëcium" arises before the polypide takes on its definite form.

3. *Origin of the Layers.* — Although later researches have only confirmed the conclusion arrived at long ago, that in Tunicates cells from all three germinal layers of the parent pass over into the bud, the facts in Bryozoa have seemed not to favor the view of the fundamental nature of this process. To be sure, Hatschek ('77, pp. 517-524) believed that he had found evidence of a condition in the budding of *Pedicellina* exactly comparable with that in the budding of Tunicates; but the more recent studies of Harmer ('86, p. 255) and Seeliger ('89) have failed to confirm his results, if they have not satisfactorily explained the source of his error.

What is the relation of the condition I have described in *Cristatella* to the question of the transmission of a part of each germinal layer to the bud, and in how far do the conditions here agree with our present knowledge of the budding process in other groups of Bryozoa? Although my results accord with Hatschek's in this, that the youngest and next older buds are intimately related, that the corresponding layers in each are derived from the same cell layers, and that the inner layer of the bud is not derived directly from the overlying ectoderm, they do not strengthen the idea of the fundamental importance of his doctrine, "Die Schichten der jüngeren Knospe stammen von denen der nächst älteren direct ab." Moreover, they afford no evidence of the accuracy of his conclusion, that the inner layer of the bud is composed of entoderm; indeed, since this inner layer does not give rise to the alimentary tract alone, as he supposed, but to the nervous system also, the facts in *Cristatella* tend to weaken his hypothesis. In order to determine finally just what the origin of the stolon from which the inner layer arises is, it will be necessary to study the origin of the first-formed polypides. This I have not yet been able to do. Our present knowledge on the subject is still in an unsatisfactory state.

Allman ('56, pp. 33, 34) has described and figured some stages in the

development of the egg, but without referring to gastrulation, or the layers involved in the first polypide.

Metschnikoff ('71, p. 508) and Nitsche ('75, p. 349) maintain that the outer layer of the embryonic "cystid" goes to form the inner layer of the primitive polypides, and that its inner layer forms the outer layer of the polypides.

Reinhard ('80^a, pp. 208-212) is more explicit concerning the early stages than preceding authors. Apparently the egg segments regularly, and undergoes embolic invagination. The blastopore closes. There is a circular groove in the anterior part of the embryo (Barrois's mantle cavity), and from the cap or "hood" which the mantle cavity surrounds, the wall of the "cystid" or colony-wall is subsequently formed. The embryo is already composed of three layers, "an outer, the tunica muscularis, and the entoderm." All three layers of the "hood" share in the formation of the polypides, but the fate of each layer is not clearly described.

Haddon ('83, p. 543) suggests that the gastrula is to be regarded as one in which the alimentary tract is retarded in development, and that the enlarged cœlomic diverticula, such as occur in *Sagitta*, etc., line nearly the whole of the so-called archenteron. From the small mass of true entoderm at the pole opposite the blastopore the alimentary tract arises. This suggestion, unfortunately, has no positive facts for its support, and could be of service only upon the assumption that the alimentary tract of the first polypide is formed from the *inner* layer of the "cystid"; but this assumption is contrary to the observation of all who have written on this subject.

Kraepelin ('86, p. 601) has also observed the "gastrulation," but he believes that it is to be interpreted as the precocious formation of an enterocoel, in which case the invagination to form the first polypide is to be regarded as the true gastrulation, the inner layer of the cystid as mesoderm, and the inner layer of the bud as entoderm.

By far the most satisfactory and complete account of the embryology of fresh-water Bryozoa is that of Korotneff, '89. The genera studied were *Alcyonella* and *Cristatella*. Since the development takes place inside of an oecium, the use of the section method is necessary for the elucidation of the details of the embryological processes. Apparently the egg segments regularly and forms a blastula. Loose cells are given off from the inner surface at one pole of this blastula. These arrange themselves in an epithelium, lying immediately inside of the ectoderm, over a part only of its inner surface; so that while the upper two-thirds

of the embryo has two layers, the lower third is one-layered. The cavity of the lower third contains some scattered cells, which, the author hints, may be representatives of the mesoderm, while the cavity in which they lie may represent an enterocœl. The author regards the inner layer of the upper two-thirds as true entoderm. The method of its formation recalls that of the entoderm of some Cœlenterata, as demonstrated by Metschnikoff. There is no epithelial invagination, such as Kraepelin maintained, and therefore the cavity which the inner layer lines cannot be regarded, says Korotneff, as an enterocœl. Later, the entire embryo becomes two-layered by an extension of the inner layer. The two polypides arise from two distinct invaginations of the double-layered wall.

Unfortunately, Korotneff does not demonstrate by figures the method of origin of the alimentary tracts of the first polypides; but there is little reason to doubt that it is essentially like that in other buds. If it is admitted that the inner layer is entoderm, as Korotneff maintains, then the entoderm takes no part in forming the digestive epithelium; but the latter is derived solely from ectoderm.

In his discussion of the theoretical bearing of his results (p. 404), the author seems to maintain that the polypide is to be regarded neither as an individual (Nitsche's view), nor, on the other hand, as an assemblage of organs homologous with organs of the same name in other groups; but rather as a new structure, developed upon the cystid, to aid in its nutrition.

In criticism of Korotneff's view, that the loose cells given off from one pole of the blastula are entoderm, I may point out that this process bears quite as much resemblance to the process of "mesenchyme" formation (as described by Korschelt for the Echinoids), as it does to the origin of the entoderm in some Cœlenterates. Compare Figs. 13 E and 182, in Korschelt und Heider's *Lehrbuch der Vergleichenden Entwicklungs-geschichte*.

Braem ('89^b, pp. 676, 677) has shown that the primary polypide of the statoblast arises from the cell layers of the statoblast, exactly as the primary polypide of the egg embryo does from those of the "cystid," and the alimentary tract is formed as in buds of *Cristatella*.

To sum up: The outer layer of the colony-wall is ectodermal in origin; the inner layer arises by an embolic (?) invagination of the blastula, and would therefore appear to be entoderm, although the possibility of its being homologous with the mesoderm in other forms is perhaps not excluded. The first polypides so arise that their inner layers are

formed by an invagination of the outer layer of the colony-wall, and their outer layer from the inner layer of that wall.

In *Endoprocta*, Seeliger ('90, pp. 176-187) has shown decisively that the inner layer of the bud is derived solely from the ectoderm, and that this inner layer gives rise to the digestive epithelium of the alimentary tract, to the nervous tissue of the brain, and to the outer layer of the tentacles. Here mesenchymatous cells, representing undoubtedly mesodermal tissue, come secondarily to surround the polypide as a loose outer tissue. In *Loxosoma* the same is probably true.

The conditions of budding in *Gymnolæmata* are more difficult to understand. In *Paludicella* the bud seems to arise as in *Phylactolæmata* (Allman and Korotneff). The same is probably true for *Alcyonidium* (Haddon, '83, p. 523, Plate XXXVIII. Fig. 23). In the *Cheilostomata*, however, the fact of the great development of a loose mesenchyme-like tissue obscures the process, and makes it difficult of interpretation. This tissue, which is known under three probably homologous terms, — "Funiculargewebe," Nitsche, "Parenchymgewebe" in part, Vigelius, and "Endosarc," Joliet, — is to be considered as representing the funicular and cœlomic tissues of *Phylactolæmata*. The most careful observations on the origin of this tissue are those of Joliet ('77, pp. 249, 250, and '86, pp. 39, 40) and Vigelius ('84, p. 76). Both authors assert that this tissue is derived from cells given off from an epithelium at the distal end of the budding individual. Vigelius ('84, pp. 19, 79) believes that this epithelium is ectodermal, and that it is the sole rudiment of this layer; but Ostroumoff ('85, p. 291) and Pergens ('89, p. 505) have shown that the ectoderm persists and secretes in its cells the calcareous ectocyst. It seems more probable, however, that the "funicular tissue" arises from the inner layer of the body-wall (Nitsche, '71, p. 37, Plate III. Fig. 5, c.), and is the equivalent of the cœlomic epithelium of *Cristatella*. The fact that many of these mesenchymatous cells conglomerate in the formation of the polypide sufficiently accounts for the origin of its outer layer of cells. The origin of the inner layer is problematical, if, as is asserted to be the case by several authors, the bud is not formed in the region of the body-wall.

It will be premature to speculate upon the significance of the facts of budding in the *Ectoprocta* until we shall have gained a more complete knowledge of the ontogeny of the group, and of the relationship of the *Cheilostomatous* to the *Phylactolæmatous* type through comparative agamogenetic studies. It may appear in the end, that, under certain circumstances, undifferentiated embryonic tissue, derived from a

certain germ layer, can assume the task of building organs in budded individuals similar to those derived from a different layer in the sexually produced individual.

Whatever may be the truth of the conclusions reached by Haddon ('83, pp. 548, 549, 552) and by Joliet ('86, pp. 54-56), that the nervous system and the alimentary tract arise from two distinct layers, or kinds of cells, in the species studied by them (and their evidence is certainly not conclusive even for these), their attempts (Haddon, '83, p. 540, Joliet, '86, p. 57) to apply their results to the Phylactolæmata are not justified by the observations which are here presented, nor by those which have been made upon most Gymnolæmata and Endoprocta.

4. *Origin of the Alimentary Tract.* — There is a curious difference between the Endoprocta and the Ectoprocta in the development of the organs of digestion. Seeliger ('89, pp. 182-184) has shown for *Pedicellina*, that the œsophagus and stomach arise as an evagination of the oral wall of the young bud, which secondarily becomes connected with the proctodæum. Haddon ('83, pp. 517, 518) has shown for *Flustra*, Barrois ('86, pp. 73-86) for *Lepralia*, Braem ('89^b, pp. 677, 678) for the statoblast polypides of *Cristatella*, and the present paper for the polypides in the adult *Cristatella*, that the œsophagus only is formed on the oral side, the stomach arising with the rectum on the anal side of the atrium. In all cases the œsophagus is formed first (Plate II. Fig. 13). A comparison of my Figure 18 with Figure 41, Plate XXX., of Hatschek ('77), shows a striking resemblance between the two. The form of the alimentary tract and the depression to form the ganglion are practically identical; and were the tentacles to arise directly from the immature lophophore arm (*br. loph.*, Fig. 18), and from the circumoral fold which has already appeared, it would be difficult to decide whether the anus opened outside or inside the circle of tentacles, — whether, at this stage, the *Cristatella* polypide were ectoproct or endoproct.

5. *Origin of the Central Nervous System.* — The only observations on the origin of the brain in Bryozoa relate to Phylactolæmata and Endoprocta. In buds of *Pedicellina*, the ganglion is formed, according to Hatschek ('77, p. 520), as an invagination of the floor of the atrium, which later becomes cut off as a hollow sac. Harmer ('85, pp. 274, 275) has studied the origin of the ganglion in the bud in *Loxosoma*. He states that it is derived from the floor of the vestibular [atrial] cavity, and (apparently on purely theoretical grounds) that this latter is ectodermic. "In a longitudinal section through a fairly advanced bud

(Fig. 15) it is seen that a narrow slit-like diverticulum of the vestibule passes behind the epistome. This diverticulum, which remains in very much the same condition throughout life, does not give rise *in toto* to the ganglion, which is merely formed by a differentiation of some of its ectodermic cells." Harmer further doubts Hatschek's account of the formation of the ganglion in *Pedicellina*, and believes that the lumen of Hatschek's hollow sac is in reality the commencement of the fibrous tissue which occupies the centre of the ganglion in the adult, and which in optical sections might easily be mistaken for an empty space. "Similarly," he continues, "Nitsche has described the ganglion of *Alcyonella* as originating as a diverticulum from the tentacle sheath. I regard it as probable that the explanation which I have suggested for *Pedicellina* will hold also for *Alcyonella*." The conditions which every student of the embryology of *Phylactolæmata* has stated since Metschnikoff's paper in 1871, and which my own results reaffirm, do not warrant Harmer's conclusions. The nerve fibres are very evident in the adult ganglion of *Cristatella*, and in addition to them there is a cavity, ontogenetically derived from the atrium, which, as Saeftigen ('88, p. 96) has also shown for *Phylactolæmata*, contains no histological elements (Plate V. Fig. 52).

6. *Origin of the Funiculus and Muscles.* — The origin of the so-called funicular tissue in *Gymnolæmata* has been described already (page 126). This same tissue also gives rise, according to Vigelius ('84, pp. 34, 35) and others, to the retractor muscles of the polypide. As I have already shown (pages 115-117, Figs. 22, 54), in writing of the origin of these tissues in *Cristatella*, the cœlomic epithelium gives off cells, some of which take on an amœboid appearance, and, uniting together, form that end of the funiculus which is attached to the colony-wall. Other cells from the cœlomic epithelium pass directly to the adjacent outer layer of the bud, to form the nascent retractor and rotator muscles. Both of these organs are, however, formed in part from cells composing the outer layer of the bud, — itself closely related ontogenetically to the cœlomic epithelium.

These facts would seem to confirm the conclusion which the similar relation of the two layers would suggest, namely, that the cœlomic epithelium of *Phylactolæmata* is the homologue of the "endosarc" of *Gymnolæmata*.

IV. Organogeny.

1. *Development of the Ring Canal.* — Nitsche ('75, p. 358) describes the ring canal as a furrow arising from the opening of each of the lophophoric pockets, and running towards the oral side of the bud. In a later stage, both layers become deeply implicated in this furrow, and the ring canal is completed by a growing together of the edges of the furrow.

Braem ('89^b, p. 679) merely states that he cannot fully agree with Nitsche's description of the formation of the ring canal.

As a result of my own studies on this subject, I have reached the conclusion that the circumoral branch of the ring canal makes its first appearance in the median plane in the oral region at about the time that the depressions of the lophophoric pockets are first indicated. The formation of both organs is preceded by a preliminary thickening of the inner layer of the bud (Plate IV. Fig. 26, *br. loph.*, and Plate III. Fig. 17, *can. crc.*). It is only later, after the lophophoric pockets have attained considerable depth, that the groove of the incipient "ring canal" appears continuously on the side of the polypide, extending from the pre-oral region to the lophophoric pockets (Plate IV. Figs. 33, 35, 37, *can. crc.*).

As indicated in the successive stages of Figures 18 and 19, Plate III., the thickening of the inner layer anterior to the mouth is followed by a fold at this point involving both layers. The fold is deepest in the pre-oral part of the median plane, and becomes shallower as it proceeds posteriorly. Finally, the outer-layer cells of the lips of the fold approach each other and fuse, thus forming a true canal (Plate IV. Fig. 33, *can. crc.*). Kraepelin ('87, p. 57, Figs. 72, 73, *qb.*) asserts that this canal does not communicate at its neural ends with the cœnocœl, but that it is always closed by a strong "Querbrücke" connecting the "Kamptoderm" with the alimentary tract. By making sections of the colony parallel to the sole, dozens of individuals are cut through the entire length of the circumoral ring canal. Although I have examined many individuals cut in this way, I have never succeeded in finding in *Cristatella* this closing "Querbrücke"; but in both young and old specimens, sections nearly corresponding to Kraepelin's Figure 72 show a perfectly uninterrupted semicircular space surrounding the œsophagus, and opening freely into the cœnocœl on each side of the brain (Plate IX. Fig. 78, *can. crc.*). I must therefore conclude that in *Cristatella* the fluids of the cavities of the circumoral branch of the ring canal, and therefore

of the tentacles also, are in free communication with the fluids of the common body cavity. As Figure 51, Plate V., shows, the posterior ends of the ring canals open into a pair of cavities which are the bases of the lophophoric pockets, and by a comparison of Figures 61-63, *can. crc.*, *can. crc.*', Plate VII., it will become apparent that they each become confluent with a furrow which passes up the lophophore arm, and from which the outer lophophoric row of tentacles is developed. Further, by a comparison of *can. crc.*", *can. crc.*", in Figures 61-63, Plate VII. (dextroristral vertical sections), and Figure 50, Plate V. (horizontal section, compare also Fig. 52, a sagittal section), it will be seen that from the tip of the lophophoric arm a groove (*can. crc.*") passes down upon the side opposite to the ascending groove (*can. crc.*'), and, reaching the base, turns abruptly anteriorly (*can. crc.*", Fig. 50), and finally, in a later stage, becomes confluent with its fellow of the opposite side in the median plane just behind the epistome and above the brain. It would be quite unnecessary for me to give figures showing the course of this supraganglionic canal (cf. Fig. 52, Plate V.). It has long been recognized, and is shown in Kraepelin's ('87) Figure 66, Taf. II. This is probably what Verworn ('87, pp. 114, 115, Figs. 20 a, 20 b, Taf. XII.) has described as a "segmental organ." Braem ('89^b, p. 679) has given to it the name "Gabelkanal." The "Ringkanal" of Nitsche is, then, to my mind, merely the circumoral portion of a groove which is elsewhere unclosed to form a proper canal and which lies at the base of all tentacles. My reason for avoiding another term for the unenclosed portion of the "canal" is, that I regard the whole as morphologically equivalent to the ring canal of *Gymnolæmata*, which is said to be closed throughout.

2. *Development of the Lophophore.* — The early stages in the formation of this organ are well known, both from the descriptions of Nitsche ('75, pp. 357, 358) and the earlier ones of Allman and others.

I have already (page 114) shown how the cavities of the lophophoric pockets become confluent between the rectum and ganglion, and how their opposed walls, formerly passing over into each other through the floor of the brain, are now anteriorly continuous by means of the new floor of the atrium, and posteriorly are fused together.

The union of the inner layers of the two opposed walls of the lophophore arms (Plate V. Fig. 44, *loph.*') continues, however, for some distance above the floor of the atrium, up to within a short distance of the tips of the young arms (Plate VII. Figs. 61, 62, *loph.*'). As the arms grow longer, the relative extent of their free and fused portions remains

approximately the same. The free ends of the arms are shown in Figure 99, Plate XI., just above *loph'*. The polypide figured here is only slightly older than that of Figure 77, Plate IX. The connection between the two arms is not one of contact merely, for in the region of fusion one can count roughly three layers of nuclei, whereas each of the two free portions of the same cell layer contains but one layer of nuclei (Fig. 99).

Before the atrial opening is formed, a separation of the two arms begins to take place. This process commences at the base of the arms, and proceeds upward as the tentacles of the inner row successively reach a certain stage of development. As the work of separation progresses, the cells of the connecting band lose their capacity for becoming stained and appear vacuolated. The vacuoles increase in size until the connection between the arms is reduced to a series of fine threads (Plate VIII. Fig. 75, *loph.'*), which are probably sundered when the tentacles of the inner row (*can. crc.*, Fig. 76) bend at right angles to their former position to become parallel to those of the outer row. In attempting to find an explanation of this process, it must first be ascertained how the arms of the lophophore grow in length. One is perhaps inclined to think of a terminal growth, but this does not take place. So far as I can judge from an examination of many longitudinal sections of the arms, cell proliferation goes on throughout the whole length of the arm, and with nearly equal rapidity in all parts. The distance between the centres of the terminal tentacles is about the same as in the case of the more fully developed proximal ones, but they are closer together in the young arm than in the adult one. This being the case, there ought to be as many (incipient) tentacles in the young as in the adult, and I find that to be, so far as I can determine, very nearly or exactly the case.

The horseshoe-shaped lophophore being characteristic of the Phylactolæmata, a study of its development is important, since it may be expected to throw light on the phylogeny of the group. We have in *Cristatella*, *Plumatella*, and *Fredericella*, a series in which the arms of the lophophore are shorter and shorter, in correspondence with other changes, by which is effected a gradual transition to the Gymnolæmata, which have a circular lophophore. In Gymnolæmata, the ring canal lies at the base of all tentacles in the adult. The anus lies outside the circle of this canal. The brain lies within the lumen of the canal.

Nitsche ('71, pp. 43-45) has given the best description extant of the

development of the lophophore in Gymnolæmata. At a very early stage, the rudiments of the tentacles, he says, are seen lying in a U-shaped line, surrounding the mouth in front, but unclosed behind. The same is true for *Paludicella* (Korotneff, '75, p. 371). The post-oral tentacles make their appearance at the posterior free ends of the row of tentacles. They are bent slightly downward, so as to be concealed by the tentacles above. At a later stage, the tentacles lying next to the anus gradually come to lie nearer to the anal side of the mouth opening, the nearly parallel lateral rows lose their compressed appearance, and a circular basin is formed whose walls are constituted by the corona of tentacles.

In *Pedicellina* (Hatschek, '77, pp. 520, 521) the tentacles arise as five pairs of papilla-like processes in the upper part of the atrium. Two additional pairs are formed later nearer the anal opening. In the adult (Nitsche, '69, p. 21) the tentacles are arranged with bilateral symmetry, and so that the plane of symmetry passes through two inter-tentacular spaces, which are thus the only unpaired spaces; they are also much broader than the others.

One might be inclined to ask by what modification of the condition of the tentacles in Endoprocta we may suppose the condition in Ectoprocta to have arisen, but the question is not a fair one. I have already (page 127) shown that the young bud of *Cristatella* has many points of similarity to a well advanced Endoproct. This similarity leads me to the conclusion that the common ancestor of the Endoprocta and Phylactolæmata more nearly resembled the former than the latter group. But the Endoprocta are not that common ancestor; rather they are themselves more or less modified descendants of it. The proper inquiry is, To what ancestral relation between tentacles and anal opening does a comparison of the ontogeny of Endoprocta and Ectoprocta point, and by what modifications of that ancestral type may the two divergent types of the present be derived? Eliminating for a moment the evidently cœnogenetic character of the lophophore arm, an early stage of either Endoprocta or Ectoprocta reveals a U-shaped band from which tentacles are to arise. This band completely encircles the mouth, and passes posteriorly as far as the anus. This is the condition of the Endoproct bud, with only five of its seven pairs of tentacles formed; it is also the condition of the *Cristatella* bud of Stage XIII. (compare Figs. 19, 44). Starting from this common condition, that of the adult Endoproct, on the one hand, was attained by the addition of two pairs of tentacles posteriorly, thus nearly completing the circlet

behind the anus. The condition of the adult Ectoproct, on the other hand, was reached by the curving oralwards, and the meeting of the free ends of the rows of tentacles between the mouth and anus, thus shutting the anus outside of their circle. In evidence of this latter assertion, I submit the following comparative statement.

As Nitsche has shown for Gymnolæmata, the tentacles on the ring canal are first arranged in two rows, placed bilaterally, and meeting in front, but not behind. Later the hindermost of the tentacles move forward and toward the median plane, thus completing the circlet of tentacles at a point behind the mouth, but in front of the anus. I believe the circumoral ring canal plus the early invaginations of the lophophoric arms in Phylactolæmata to be homologous with the ring canal of Gymnolæmata in its early stage; like the latter, it is closed in front, but has two free ends behind. The difference lies in the greater development of the posterior ends of the canal, which latter have become thrown into a vertical fold to afford space for more tentacles. At this stage of development it would be difficult to say whether the anus opened within or without the corona of tentacles. As in Gymnolæmata the circle is completed by a movement inward of the posterior tentacles, so in Phylactolæmata the corona of tentacles is completed in front of the anus by the two anterior processes, *can. crc.*''', Figure 50 (cf. Fig. 44), of the lophophore arm, which come to unite just behind the epistome, Figures 52, 81, *can. crc.*'''. The lumen of this process of the lophophore arm thus forms that portion of the ring canal which, as I shall show directly, is the morphological equivalent of the most posterior portion of the ring canal in Gymnolæmata. The tentacles which arise from this portion of the ring canal are ontogenetically, and therefore phylogenetically, the youngest. As in Gymnolæmata, so here the moving forward of the most posterior tentacles obliterates the basin-like floor of the atrium, such as we see in Endoprocta, and leaves the anal opening far outside the circlet of tentacles.

The answer to the question, How may the horseshoe-shaped tentacular corona of Phylactolæmata be homologized with circular ones? is involved in the answer to the preceding query. Nitsche ('75, p. 357) believed the lophophoric arms to be "primary tentacles," and the tentacles borne on them to be secondary tentacles, "Gar nicht ohne Weiteres mit den Tentakeln der Infundibulata von GERVAIS zu vergleichen." The only evidence which he offers in support of his theory is the fact that the tentacles on the lophophore arm arise later than the arm itself.

The tentacles of *Phylactolæmata* may be distributed into two groups. The first includes those which arise from the circumoral branch of the ring canal. The ring canal, from which they spring, begins to be formed at nearly the same time as the lophophoric arms. These tentacles are undoubtedly homologous with those of the same region in *Endoprocta* and *Gymnolæmata*. The second group of tentacles includes those which are borne upon the lophophore arms and upon the supraganglionic ring canal. Are these comparable with the posterior tentacles of *Gymnolæmata*? I believe they are, and for the following reasons. Nitsche's reason for supposing that they are not is unsatisfactory, since, if we regard the lophophore arms as mere upward folds of the wall of the ring canal, we should expect to have the tentacles arise later than the arms. The fact that the tentacles of the lophophore arm arise much later than those of the circumoral region is what we should expect, since the posterior tentacles arise later than the circumoral ones in both *Endoprocta* and *Gymnolæmata*, — a criticism which Hatschek ('77, p. 541) has already applied. In direct support of my belief are the facts, (1) that the ring canal is continuous along two sides of the lophophore arms, which would be the case if they were mere upward folds of the wall of the ring canal; (2) the structure of the tentacles is the same as that of the oral ones, and the relation of their intertentacular septæ to the ring canal of the arms is the same as that of the septæ of the oral tentacles to their ring canal, as Kraepelin ('87, pp. 55, 56) has shown. If both circumoral and lophophoric tentacles find their homologues in *Gymnolæmata*, we have only to conceive of an elongation of the posterolateral angles of the lophophore of *Gymnolæmata*, after the forward movement of the posterior tentacles, to effect the condition which is found in *Phylactolæmata*.

The significance of the fusion of the lophophore arms is difficult to determine. I had thought it might be possible to find a phylogenetic explanation for it, by regarding the unfused tips of the arms in *Cristatella* as homologous with the short arms of *Fredericella*. In studying *Plumatella*, however, where the length of the lophophore arms is intermediate between that of *Cristatella* and *Fredericella*, I have been able to find no trace of this fusion. It does exist, however, in *Pectinatella*. I have had no material of *Lophopus*, upon which it is important to study this point. The evidence so far seems to indicate that this fusion of the arms during the period of their development is a secondarily acquired adaptation to some condition concerning the nature of which I am ignorant.

3. *Development of the Tentacles.* — Nitsche ('75, p. 359) observed that both layers of the bud went to form the tentacle in Phylactolæmata, and that the inner layer was derived from the outer layer of the polypide; the outer, on the contrary, form the inner cell layer. He states, moreover, as already mentioned, that the oral tentacles arise first, then those of the outer row of the lophophore arms, of which the basal are fully formed before the terminal ones. The tentacles of the inner row, he says, are formed last, and in *Alcyonella* are yet lacking when the polypide is first evaginated.

My own observations confirm in general those of Nitsche. The longest tentacles in a polypide of about the age of that shown in Figure 77, Plate IX., are those arising from the region of transition from the circumoral ring canal (*can. crc.*) to the outer lophophoric ring canal (*can. crc.'*). The tentacles lying near the median plane, and in front of the mouth, are somewhat shorter than these ($75\ \mu:52\ \mu$). The tentacles situated near the proximal extremity of the inner lophophoric ring canal (*can. crc.''*) are still shorter ($50\ \mu$). Those situated at the tips of the lophophore arms are at this stage about $30\ \mu$ in length. The tentacles behind the mouth, arising from the supraganglionic part of the ring canal (*can. crc.'''*), are shortest of all at this stage ($15\ \mu$).

The two layers which, as we have seen, go to form the upper wall of the ring canal in all its parts, are the ones which give rise to the tentacles. In Figure 74, *ta.'*, Plate VIII. (compare Fig. 51, *ta.'*), young oral tentacles are cut transversely at different heights. The circumoral part of the ring canal is seen at a point (*can. crc.*) near which it opens into the cavity of the lophophore arm. The plane of the section passes obliquely upward and anteriorly from this point. The most posterior tentacle in the lower part of the figure is cut at the base. The calibre of the canal (including its walls) is evidently much enlarged at this point. The enlargements of the canal at the base of the tentacles are seen also in Figure 78, *can. crc.*, Plate IX. The more anterior tentacles in Figure 74 show the two layers well marked, but as yet enclosing no lumen. Since the tentacles arise from the ring canal at intervals only, the ring canal is a tube (or groove) whose lumen is alternately constricted and expanded laterally as well as vertically. The lumen is, indeed, often so small between the tentacles that the ring canal appears divided into separate chambers by a series of transverse septæ, which, however, are always penetrated by an opening (Fig. 78, *can. crc.*). Figures 73 and 77, *ta.'*, show, in longitudinal section, successive stages in the development of the oral tentacles. The formation of tentacles begins by a rapid cell

proliferation at intervals in the upper wall of the ring canal; thus a projection is formed at each of these points, which constantly elongates to form the tentacle. Figures 70 and 69 (Plate VII.) are longitudinal sections of two later stages in the development of tentacles. The inner layer, *ex.* (Fig. 70), becomes gradually thinner as the tentacle grows older, and its cells finally become thread-like (Fig. 69, *ex.*).

Figure 81 (Plate IX.) shows the arrangement of the tentacles about the mouth and over the ganglion in a young polypide. The supraganglionic part of the ring canal is cut tangentially just behind the epistome (*can. circ.*'''). I have often noticed that, in polypides of about the age of that of Figure 77, or older, certain of the nuclei seen in a cross section of a tentacle stain more deeply than the others. These nuclei are usually two or three in number on each of the lateral surfaces of the tentacles. They are evident in Figure 81. I do not know what this difference in staining properties signifies. Vigelius ('84, p. 38, Fig. 23) describes and figures a condition of the nuclei in *Flustra*, as seen on cross-section, which is similar to that just described. The deeply staining nuclei in *Flustra* lie on the inner face of the tentacle, are larger than the others, and belong to cells which possess no cilia.

Nitsche ('71, p. 43) described the development of the tentacles in *Flustra* as though they were derived exclusively from the inner layers of the bud; but Repiachoff ('75^a, pp. 138, 139, '75^b, p. 152) showed that in Cheilostomes both cell layers of the bud took part in their formation, and he figures an early stage which is quite similar to my Figure 70.

4. *Development of the Lophophoric Nerves.*— It has long been known that a large nerve passes along the middle of the upper wall of each lophophore arm, connecting proximally with the corresponding side of the ganglion. No observations have been made, so far as I know, upon the origin of this organ. Evidently there are, *a priori*, two possibilities. Either (1) the lophophoric nerve is formed by a direct outgrowth of the ganglion, or (2) it arises in place from the inner layer of the bud, which, since it here forms the outer layer of the lophophoric pocket, is the same as that from which the ganglion itself is constructed. By a careful study of this nerve in many stages of development, and from sections in different directions, I have come to the conclusion that it arises as an outgrowth of the walls of the ganglion, and that it penetrates between the outer and inner layers of the arm.

The facts which have led me to this conclusion are these. First, during the formation of the brain, soon after its lumen is cut off from its connection with the atrium, its cells begin to divide rapidly (Plate V.

Fig. 51, Plate VII. Figs. 63, 68); but that the new cells so formed do not all remain in the brain is indicated by the fact that the brain does not increase very rapidly in size. (Compare Plate III. Fig. 19, and Plate IX. Fig. 77.) This rapid cell division would be inexplicable upon the assumption of an origin *in situ*. Secondly, at an early stage the lophophoric nerve is already seen extending from the brain to the adjacent inner layer, with which it remains in contact. A longitudinal section through the middle of this nerve shows a prolongation of the lumen of the brain extending into it, so that its upper wall passes directly into the upper wall of the brain, and its lower wall into the corresponding part of the central organ (Plate VII. Fig. 68, *lu. gn., n. loph.*). The proximal part of the lophophoric nerve is thus to be regarded as a pocket of the brain. The existing condition is not what we should expect if a cord of cells derived from the outer layer of the lophophoric arm had secondarily fused with the brain. Thirdly, I have never found any good evidence that cells were being given off from the outer layer of the arm at its tip to form the nerve, where we should look for such a process, if anywhere; on the contrary, the nerve is quite sharply marked off from the outer layer at this point, as will be seen by reference to Figures 64-67 (Plate VII.). These figures represent successive transverse sections from a young lophophore arm of about the stage of development of that shown in Figure 71. Figures 65-67 were drawn from one arm in about the position indicated by the lines 65-67 in Figure 71. Figure 64 was drawn from the opposite arm of the same individual, and in about the region of Figure 65. In Figures 64 and 65 there is a small space between the nerve (*n. loph.*) and the overlying cells of the inner layer (*i.*). This may be due to shrinkage, but in any event it indicates a complete independence between the two cell masses which it separates. Over the nerve the cells of the layer *i* are shorter than elsewhere. This might be considered as an indication that the cells had recently divided in order to give up cells to the nerve, which, on this assumption, would be formed *in situ*. Three appearances, however, indicate that the cells of the layer *i* have been rather subjected to crowding at this point, as though by a mass of cells forcing their way between them and the layer *ex.*, and gradually increasing in volume. (*a.*) The surface of the layer *i* is raised above the general level directly above the nerve. (*b.*) The cells of the layer *i* are somewhat broader over the nerve than elsewhere, and the nuclei are shorter, but thicker. These are the conditions which we should expect in an epithelium subjected to pressure by the intrusion of a mass of cells at its base, for in volume the crowded cells compare

fairly with their neighbors, whereas, if they had by division given rise to nerve cells, they should all be smaller. (c.) In Figure 67, which is a section immediately in front of the advancing tip of the nerve, the position corresponding to that opposite the nerve in the preceding sections is indicated by an asterisk (*). The nuclei are here crowded together, indicating pressure. Fourthly, there is a considerable difference in size between the nuclei of the cells of the layer *i.* of the lophophore and the nerve cells. This is not what one would expect upon the assumption of the formation of the nerve directly from the overlying cells. Fifthly, a longitudinal section through the young lophophoric nerve (Plate VII. Fig. 71) shows a more active cell division in it than in the walls of the arm (compare Fig. 64, *n. loph.*), and a crowding together of nuclei of the outer layer of the arm, *i.*, at its distal end, rather than a passage of nuclei into the nerve.

The conclusion to which I have arrived from considering these facts is that the *peripheral nervous system in Phylactolamata arises from the brain as an outgrowth of its walls.*

5. *Development of the Epistome.* — The epistome was regarded by Lankester at one time ('74, p. 80) as homologous with the foot of Mollusca, and on another occasion ('85, p. 434) as representing the preoral lobe of Annelids, — a view for which Caldwell ('83) first produced evidence from comparative embryology. In view of such divergent opinions, and of the occurrence of an organ which is possibly its homologue, in quite aberrant genera, such as Phoronis, Rhabdopleura, etc., a careful consideration of its origin and development is desirable.

After the ganglion is fully formed, its oral face remains in contact in front with the posterior wall of the œsophagus (Plate V. Fig. 52, Plate IX. Fig. 77), and on each side with the outer wall of the lophophoric pockets by means of the lophophoric nerves (Plate VII. Fig. 63, *n. loph.*). The outer layer of the bud penetrates between the ganglion and rectum, but not between the ganglion and the œsophagus (Fig. 51,*). This layer also comes to lie between the floor of the atrium above, the ganglion below, and the lophophoric nerves on either side, having made its way in from behind as a double cell-layer enclosing a flat cavity (Plate V. Fig. 52, Plate VI. Fig. 56, Plate VIII. Fig. 74, *can. e stm.*). My description of the process by which the inner layer comes to envelop the ganglion above and behind differs considerably from Nitsche's, already quoted (page 114). As the ganglion becomes farther removed from the floor of the atrium, the cavity above it (*can. e stm.*) enlarges, and the two lateral walls of this canal, each composed of

two layers of cells, both belonging to the outer layer of the bud, form the "Verbindungsstrang des Ganglions mit dem Lophoderm" of Kraepelin ('87, p. 63, Taf. II. Fig. 59, *vs.*). (See Plate V. Fig. 51, Plate VI. Fig. 56, and Plate IX. Fig. 80,*) This canal is the only one by which communication between the body cavity and the cavity of the epistome can occur. It may be called the *epistomic canal* (Plate V. Fig. 52, Plate VIII. Fig. 72, *can. e stm.*).

The epistome proper arises at the point where the epistomic canal ends blindly, above and in front of the brain (Plate VIII. Fig. 73, Plate IX. Fig. 77, *e stm.*); it is a pocket, the outer wall of which is continuous on its under surface with the œsophageal epithelium, and on its upper surface with the floor of the atrium. The growth of this organ is disproportionately great after the first evagination of the polypide. That part of its wall which is turned towards the alimentary tract is then much thicker than the remaining part; it forms the posterior wall of the pharynx (Plate VIII. Fig. 72, *e stm.*; compare Plate IX. Fig. 81). Is the epistome innervated by fibres from the brain, as maintained by Hyatt ('68, pp. 41-43)? I have not succeeded in finding such fibres, and the conditions of the formation of the epistome, cut off as it is from the brain at every point, make such a connection improbable.

Allman ('56, Fig. 8, Plate XI.) and Korotneff ('75, p. 371) have shown for *Paludicella*, and Nitsche ('71, p. 44) has shown for *Flustra*, that an epistome-like fold occurs at an early stage of development, but is absent in the adult. Such an organ has been described by Allman ('56, p. 56) and other observers in *Pedicellina*, and it is still more prominent in *Loxosoma*, in which the relation of the epistome to the body cavity is similar to that in the *Phylactolæmata*.

The constant occurrence of this organ in the development of *Bryozoa*, and its presence in so many aberrant genera which seem to be somewhat allied to this group, can only be interpreted, it seems to me, as signifying that it is an ancient and morphologically important organ. The manner of its development in *Cristatella* seems to throw very little light, however, upon its significance; it arises rather late, and does not become of any considerable size until the atrial opening is made.

6. *Development of the Alimentary Tract.*—The later development and histological differentiation of the alimentary tract have not been heretofore carefully studied.

At the stage at which we left the alimentary tract (Plate III. Fig. 19) only two parts were clearly differentiated, the œsophagus and the intes-

tine. In the next stage shown (Plate VIII. Fig. 73), further changes are seen to have taken place. The most prominent is the down-folding of the lower wall of the intestine at its middle region to form the cœcum. Even at this early stage histological differentiation of the cells of this region has occurred to such an extent that the lumen of the cœcum is nearly obliterated by the great elongation of some of the cells lining it. This condition of affairs will be understood by studying the cross section of the cœcum at a later stage, as shown in Figure 94, Plate X. The cavity of the rectum has also enlarged, and its cells have taken on the regular columnar appearance which exists in the adult.

At a still later stage (Plate IX. Fig. 77), the position of the cardiac and pyloric valves, separating respectively the œsophagus (*œ.*) from the stomach (*ga.*), and the cœcum (*œ.*) from the rectum (*rt.*), is clearly indicated. The blind sac is still further elongated and well differentiated from both stomach and rectum. In order to attain the adult condition (Plate VIII. Fig. 72), the oral portion of the alimentary tract has merely to become divided, by a difference in the character of its cells, into pharynx (*phx.*) and œsophagus (*œ.*), the stomach (*ga.*) to increase in diameter, and the blind sac (*œ.*) to elongate. The anus (*an.*) finally comes to lie at the apex of a small cone, or sphincter valve.

The histological changes which the cells of the different parts of the alimentary tract undergo are considerable, and will be treated of in order, beginning with the

Œsophagus. — At a stage a little later than Figure 77, the œsophagus, as is shown in Figure 84, Plate X., has a small diameter relative to that of the rest of the alimentary tract (cf. Plate VIII. Fig. 72, *œ.*), and its inner lining is composed of high columnar epithelium, like that of the oral groove. The shape of the cells is not greatly different in the adult; but they become vacuolated, and since these vacuoles lie near the base of the cells, and either nearer to or farther from the lumen than the nuclei, the latter acquire that irregular arrangement referred to by Verworn ('87, pp. 111 and 112).

Stomach. — Figure 93 (Plate X.) represents a section across the stomach immediately below the cardiac valve, from the same individual as that from which Figure 84 was taken. The proximal ends of all cells stain more deeply than the distal ends, but the cells are all alike as far as regards receptivity to stains. Already, in certain regions, the cells are higher or lower than the average, and have even begun to group themselves as typical ridge- and furrow-cells. Figure 82 is a section through the same region as Figure 93, but from an adult individual. The ridge-

cells are distinguishable from those of the furrows by their greater height, their weaker attraction for dyes, and their vacuolated and granular appearance. Moreover, the cell boundaries of this epithelium are gradually lost. Kraepelin ('87, p. 51) has argued that the elongated cells are the true digestive cells, and that the deeply dyed cells of the furrows are, functionally, liver cells.

Cæcum. — Figure 94 is from a cross section of the cæcum at the stage of Figures 84 and 93. The cells are more differentiated here than at any other part of the alimentary tract. They stain uniformly, however, except for a narrow light zone next to the lumen, and all reach to the muscularis. The digestive cells are swollen at their free ends; the liver cells, on the contrary, are thickest at the base. Figure 83 is from a section of the proximal part of the cæcum of an adult. The changes which the cells have undergone are of a similar character to those experienced by the gastric epithelium, only there has been an exaggeration in this region of the features shown by the stomach. Figure 85 represents a section near the blind end of the cæcum of an adult. The diameter of the tube is smaller here than in the section last described, but the inner epithelium is thrown into still higher ridges and more profound furrows. Nearly all of the cells, however, seem to extend to the muscularis. The "liver" cells do not extend so far towards the blind end of the cæcum as this region. The cytoplasm is not at all stained. Evidently, here the process of digestion reaches a maximum. The circular muscles of the muscularis are *striped*, and are developed here to an extraordinary degree, and the cœlomic epithelium is greatly thickened, another evidence, it seems to me, of the intimate relation of this layer to the muscularis. The number of ridges is not constant in different parts of the alimentary tract of the same individual, and varies somewhat for the same region in different individuals. In sections corresponding in position to Figure 83, I have, however, usually found six ridges.

7. *Development of the Funiculus and Muscles.* — It has already (page 117) been pointed out that the fixed ends of both the funiculus and muscles originate at a great distance from their position in the adult. Thus the funiculus originates upon the *oral* face of a young bud. As this bud grows older, the fixed end of its funiculus becomes gradually farther and farther removed from its neck towards the margin, until finally the funiculus is inserted upon the colony-wall at the margin, or even upon the sole. So the retractor and rotator muscles arise together on each side of the polypide and in the angle formed by the colony-wall and the radial partitions. Later (Plate V. Figs. 44, 45, *mu. ret.* + *rot.*)

they are found on the partitions immediately below the colony-wall. Still later (Plate VI. Fig. 59, *mu. rot.*, *mu. ret.*) we see them on the lower portion of the partition, and finally (Fig. 56, *mu. rot.*, *mu. ret.*) they are found attached to the sole, at some distance, it may be, from the radial partition.

The question arises at once, How do these changes of position take place? Examination shows that the union between the cœlomic epithelium and the cells of that portion of the funiculus which is attached to the roof is very slight after the funiculus has passed to some distance from the mother polypide. Although occasionally I have seen the cells of the fixed end closely applied to the cœlomic epithelium, the only connection between the two is usually effected by means of amœboid cells (Plate V. Figs. 46-48, *cl. mi.*). On cross sections of the fixed end of the funiculus these cells (Fig. 49, *cl. mi.*) are seen to surround it as a loose layer, and in longitudinal sections some of the amœboid cells are seen to be connected with the cœlomic epithelium. It is difficult to determine the origin of these cells, but they have the position and character of the cells of which the funiculus was exclusively composed before the entrance into it of the ectodermal plug described by Braem. The only explanation of the migration of the funiculus which occurs to me has been suggested by the facts given above; namely, that the "migratory cells," by which the funiculus is attached to the cœlomic epithelium, change their position, carrying with them the funiculus. Remembering that the cœnocœl is filled with a fluid in which the funiculus floats, and that by the growth of the funiculus it is elongated in proportion as the distance from its origin to the cœcum increases, this hypothesis does not seem improbable, although its truth can hardly be tested by the study of preserved material. When the funiculus has reached its permanent position its attachment to the cœlomic epithelium is more intimate. Meanwhile the end attached to the polypide has become more and more attenuated (Plate IX. Fig. 77, *fun.*), until, in the adult, I have usually been unable to discover any attachment. In any case, it must certainly be broken when the polypide begins to degenerate.

The migration downward of the ends of the muscles which are attached to the partition is even more difficult of explanation. During this migration their point of origin seems to be in the muscularis of the partition itself. The fixed point of the muscle in the adult is probably in the muscularis of the sole, since I have traced muscle fibres through the cœlomic epithelium, and to the muscularis (Plate VI. Fig. 58, *mu.*

ret.). The insertion is in the muscularis of the polypide (Fig. 56), but I have not been able to determine the precise relation between the muscle fibres of the great cœlomic muscles and those of the muscularis. A comparison of Figures 44, 59, and 56 shows quite plainly that both the retractor and the rotator muscles originate from a common mass of muscle cells, and become distinct from one another by a separation of their points of attachment to the polypide. The retractor muscles (*mu. ret.*) are attached to the œsophagus immediately below the ganglion (Plate IX. Fig. 78); the rotator muscles (*mu. rot.*), on the contrary, to the lateral walls of the opening leading from the cœnocœl (*cœn.*) to the cavity of the lophophore arms. These two regions are near to each other in the young polypide, but become constantly more widely separated with the growth of the lophophore. Compare Figure 78 with Figures 74 (Plate VIII.) and 51 (Plate V.), which are younger stages, cut somewhat above the level of Figure 78, and more than twice as highly magnified.

I have been able to obtain in thick sections various stages in the development of the muscle fibres, some of which are shown in Figures 89 to 92 (Plate X.). In the earlier stages, all parts of the muscle cell stain uniformly in cochineal. Later, the cell body becomes differentiated into two portions, easily distinguishable by their different receptivity to the dye. The more retractile portion becomes greatly elongated, highly refractive, and incapable of being stained. A mass of indifferent protoplasm, including the nucleus, still remains stainable (Fig. 90). The undifferentiated portion continues to diminish relatively to the whole mass of the cell, which has greatly increased in size, until little remains but the nucleus, placed on one side of the muscle fibre (Figs. 91, 92). Figure 92 is one of the retractor muscle fibres, in a partly contracted state. The end placed uppermost in the figure was that which abutted upon the muscularis of the œsophagus. Its more intimate relation to the muscularis could not be traced.

8. *Origin and Development of the Parieto-vaginal Muscles.*—These consist of two sets, the lower, or *posterior*, and the upper, or *anterior*. The posterior arise earlier. At about the time when the neck of the polypide begins to disintegrate in order that the polypide may become extrusible, a disturbance is seen in the cells of the outer layer of the kamptoderm immediately below the neck of the polypide, and in the cœlomic epithelium opposite to them (Plate XI. Fig. 97, *mu. inf.*). As a result, several cells of each layer become organically connected with those of the opposite layer, and give rise to muscle cells. A later stage of

such a process is seen at Figure 98. By the time the atrial opening is established these cells have become plainly muscular (Plate IX. Fig. 79). Farther up in the angle of attachment of the kamptoderm to the roof of the colony, the coelomic epithelium and the outer layer of the bud are both seen to be somewhat disturbed (Fig. 97, *mu. su.*). At different points, a single one of these cells reaches across, and later becomes differentiated into a genuine muscle cell (Fig. 99, *mu. su.*). Of these there may be three rows.

9. *Disintegration of the Neck of the Polypide.*—The neck of the polypide, having fulfilled its function as the most important part of the stolon, must now give way to allow of the extrusion of the nearly developed polypide. The first indication of this process is the formation within the cells of the neck of a secreted substance (*cp. sec.*'), apparently like the secreted bodies of the ectoderm. This metamorphosis first involves the outer and middle cells of the neck only (Plate XI. Fig. 97, *cev. pyd.*). Later (Plate IX. Fig. 77, *of. atr.*) a depression occurs in the ectoderm. This is due, I believe, to a cessation of cell proliferation at the centre, although it remains active at the edges of the neck. The depression gradually deepens until the atrium is closed by a thin layer of cells only (Fig. 98). The cells of the side of the neck do not disintegrate, but go to form the "Randwulst" of Kraepelin ('87, p. 40). The cells of this region remain unmetamorphosed. Only a thin layer of cells now stands between the polypide and the outside world. This ruptures, as is shown in Figure 99, and by the relaxation of the muscularis, which is thickened about the atrial opening into a sphincter (Fig. 98, *sph.*), the polypide is ready to expand itself.

10. *Development of the Body-wall.*—As already stated (page 117), Braem believes that the whole body-wall in *Alcyonella* is derived from the neck of the young polypide, after it has begun to give rise to daughter polypides; and I have given my reasons for believing that in *Cristatella* a portion of it at least is derived from the margin.

In addition to this, cells are undoubtedly added to the body-wall, as Braem states, after the time of origin of the buds. Particularly after the formation of the median bud, the neck appears to continue to furnish cells to the ectoderm. Figure 73,* Plate VIII., shows such a mass of cells. Later stages show that these cells secrete a gelatinous substance within their protoplasm (*cp. sec.*', Plate XI. Figs. 97, 98); they gradually increase in width and height from the neck outward (Figs. 97-99), and at the same time become more and more completely metamorphosed. The result of the addition of these cells from the neck of the polypide is to

carry the body-wall at the region of the atrial opening to a considerable height above the level of that portion of the roof lying between polypides. (Compare Fig. 73, Plate VIII.; Figs. 98 and 99, Plate XI.) This method of origin of the body-wall is of much less importance in *Cristatella* than in *Acyonella*, since the extent of the proper body-wall about the atrial opening is much less in the former than in the latter case.

The development of the gelatinous bodies deserves further attention. Kraepelin ('87, p. 24) concluded, from a study of the condition in a statoblast embryo, that they are formed by a metamorphosis of the cell protoplasm, beginning at the outer end of the cylindrical cell, and finally involving, in some cases, the entire cell, together with its nucleus. Some appearances which I have noticed in the ectoderm of *Cristatella* lead me to conclude that the origin is not always so simple as Kraepelin describes. Figure 79, Plate IX., shows at *cp. sec.* a number of small gelatinous masses occurring at various regions in the protoplasm. Such an appearance is quite common, and must be interpreted, it seems to me, as the formation of the gelatinous balls by an intra-cellular metamorphosis of the cytoplasm. The balls, flowing together, produce the larger masses. The metamorphosed matter from several cells may also fuse into one mass (Plate VI. Fig. 55, *cp. sec.*). The final result of this process of cell metamorphosis in the ectoderm is a frame-work of old cell walls, having a thin layer of protoplasm and nuclei at its base, and enclosing the great gelatinous balls. Such a condition exists near the centre of the colony between adult polypides, and is shown in Figure 100, Plate XI.

Summary.

1. Most individuals give rise to two buds, of which one forms a new branch, the other continues the ancestral branch.
2. The median buds migrate away from the parent polypide to a considerable distance before giving rise to new buds.
3. The descendants of equal age from common ancestors are arranged similarly in the same region of the colony.
4. New branches are formed upon either side of ancestral branches.
5. The greater the difference in age between the youngest and the next older bud, the greater the distance between the points at which they begin to develop.
6. In typical "double buds," both polypides arise from a common mass of cells at the same time. From the neck of old polypides a stolon-

like process of cells is given off to form median buds. Between these two extreme types, intermediate conditions occur.

7. The alimentary tract is formed by two out-pocketings of the lumen of the bud in the median plane, one forming the œsophagus, the other the rectum and stomach. The blind ends of these two pockets fuse, and thus form a continuous lumen.

8. The central nervous system arises as a shallow pit in the floor of the atrium; the pit becomes closed over by a fold of the inner layer only of the polypide, which thus forms a sac, the walls of which become the ganglion.

9. The kamptoderm arises by the transformation of the columnar epithelium of the two layers of the wall of the atrium into pavement epithelium.

10. The funiculus arises from amœboid cells derived from the cœlomic epithelium.

11. The retractor and rotator muscles arise together from the cœlomic epithelium of both body-wall and bud, and in the angles formed by the radial partitions and the body-wall.

12. The wall of the colony grows by cell proliferation at its margin.

13. The radial partitions arise as follows: certain muscles of the muscularis at the margin of the colony leave the latter, and are carried into the cœnocœl, taking with them a covering of cœlomic epithelium.

14. Budding in *Cristatella* presents conditions transitional between direct and stoloniferous budding.

15. Throughout the group of Bryozoa, the youngest and next older buds are intimately related, and the place of the origin of the younger buds relatively to the older is determined by a definite law.

16. *Cristatella* differs from *Alcyonella* in possessing a region of the colony-wall, — the tip of the branch, — which grows independently of the polypides.

17. Each of the layers of the younger bud arises from a part of the same cell mass as that which gave rise to the corresponding layer of the next older bud.

18. The digestive epithelium and the nervous tissue are both derived from one and the same layer of cells, the inner layer of the bud.

19. The alimentary tract of *Cristatella* at an early stage is similar to that of a young *Endoproct*.

20. Harmer's conclusion, that the ganglion of *Phylactolæmata* arises exactly as in *Endoprocta*, is not confirmed.

21. The "ring canal" lies at the base of all tentacles.

22. The circumoral region of the ring canal in *Cristatella* is in free communication with the *cœnocœl* in all stages of development; and not closed, as maintained by Kraepelin.

23. The two arms of the lophophore arise independently of each other. Their adjacent surfaces undergo a secondary fusion, which persists until the inner row of tentacles is about to be formed on the lophophore. The two arms then become entirely separate.

24. The ancestor of *Bryozoa* probably possessed a U-shaped row of tentacles, encircling the mouth in front, and ending freely behind near the anus.

25. The tentacles near the mouth are phylogenetically the oldest.

26. Both layers of the bud are involved in the formation of the tentacles.

27. The lophophoric nerves arise as outgrowths of the central ganglion, which make their way into the lophophore arms.

28. The epistome arises as a fold continuous with the wall of the *œsophagus* below and the floor of the atrium above, and it communicates with the *cœnocœl* by means of the epistomic canal.

29. The *cœcum* of the alimentary tract, which occurs only in *Ectoprocta*, is produced relatively late in the ontogeny by an out-pocketing of the lower wall of the alimentary tract at the free end of the polypide.

30. The funiculus migrates (probably with the aid of amœboid cells) from the roof of the colony to the margin, or even to the sole.

31. The "origins" of the retractor and rotator muscles migrate along the radial partitions from roof to sole. The separation of the two muscles takes place secondarily as their points of insertion separate.

32. The parieto-vaginal muscles arise from the *cœlomic* epithelium of the body-wall and polypide.

33. The disintegration of the neck of the polypide is begun by a metamorphosis of the protoplasm of its cells. The metamorphosed cells break away, leaving the atrial opening.

34. The part of the body-wall lying around the atrial opening arises by proliferation of cells derived from the neck of the polypide.

35. The ectodermal cells become metamorphosed by an intercellular secretion of small "Gallertballen," which fuse to form the larger ones. Often the contents of more than one cell fuse into a single large mass.

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EXPLANATION OF FIGURES.

All figures were drawn with the aid of a camera lucida from preparations of
Cristatella mucedo.

ABBREVIATIONS.

<i>An.</i>	Anal side of polypide.	<i>mu.</i>	Muscularis.
<i>an.</i>	Anus.	<i>mu. inf.</i>	Inferior parieto-vaginal muscles.
<i>atr.</i>	Atrium.	<i>mu. lg.</i>	Longitudinal muscle fibre of muscularis.
<i>br. loph.</i>	Lophophore arm.	<i>mu. ret.</i>	Retractor muscle of polypide.
<i>can. circ.</i>	Ring canal, circumoral part.	<i>mu. rot.</i>	Rotator muscle of polypide.
<i>can. circ.'</i>	Ring canal, outer lophophoric part.	<i>mu. su.</i>	Superior parieto-vaginal muscles.
<i>can. circ."</i>	Ring canal, inner lophophoric part.	<i>mu. tr.</i>	Transverse (circular) muscle fibre of muscularis.
<i>can. circ.'''</i>	Ring canal, supra-ganglionic part.	<i>n. loph.</i>	Lophophoric nerve.
<i>can. e stm.</i>	Epistomic canal.	<i>nu. ml.</i>	Nucleus of muscle fibre.
<i>cav. loph.</i>	Cavity of lophophore arm.	<i>œ.</i>	Œsophagus.
<i>cev. pyd.</i>	Neck of polypide.	<i>of. atr.</i>	Atrial opening.
<i>cl. fun.</i>	Young cells of funiculus.	<i>om.</i>	Ovum.
<i>cl. mi.</i>	Migratory cells.	<i>Or.</i>	Oral side of polypide.
<i>cl. mus.</i>	Young muscle cells.	<i>or.</i>	Mouth.
<i>œ.</i>	Cœcum.	<i>pam. atr.</i>	Floor of atrium.
<i>cæn.</i>	Cœnocæl.	<i>pam. gn.</i>	Floor of ganglion.
<i>cp. sec.</i>	Secreted bodies of ectoderm.	<i>phx.</i>	Pharynx.
<i>cta.</i>	Cuticula.	<i>pyd. [i., ii., &c.]</i>	Polypide.
<i>di sep.</i>	Intertentacular septum.	<i>pyd. fili.</i>	Daughter polypide.
<i>di sep. r.</i>	Radial septum of colony.	<i>pyd. ma.</i>	Mother polypide.
<i>ec.</i>	Ectoderm.	<i>rt.</i>	Rectum.
<i>e stm.</i>	Epistome.	<i>sol.</i>	Sole.
<i>e t. cæl.</i>	Cœlomic epithelium.	<i>sph.</i>	Sphincter.
<i>ex.</i>	Outer layer of bud.	<i>sul. or.</i>	Oral groove.
<i>fun.</i>	Funiculus.	<i>ta.</i>	Tentacle.
<i>ga.</i>	Stomach.	<i>ta.'</i>	Oral tentacle.
<i>gn.</i>	Ganglion.	<i>tct.</i>	Roof of colony.
<i>i.</i>	Inner layer of bud.	<i>tct. gn.</i>	Roof of ganglion.
<i>kmp. drm.</i>	Kamptoderm.	<i>vac.</i>	Vacuole.
<i>loph.'</i>	Place of union of arms of lophophore.	<i>vlv. cr.</i>	Cardiac valve.
<i>lu. gm.</i>	Lumen of the bud.	<i>vlv. py.</i>	Pyloric valve.
<i>lu. gn.</i>	Lumen of the ganglion.		

PLATE I.

- Fig. 1. A portion of the lateral rim of a colony. An optical section taken just below the roof of the colony, showing the arrangement of polypides. $\times 72$.
- " 2. Origin of the stolon (I.) from the neck of a mother polypide of about Stage XII. (Fig. 18). Sagittal section of mother polypide. The margin of the colony is to the left. $\times 390$.
- " 3. Earliest stage in the origin of a bud from a young mother polypide. Sagittal section. Margin to left. $\times 390$.
- " 4. Origin of a bud from a mother polypide of about the age of that of Fig. 3. Sagittal section. The margin of the colony is to the right of figure. $\times 390$.
- " 5. Sagittal section of a double bud. Margin of colony to the left. $\times 390$.
- " 6. Later stage in bud formation of same type as Fig. 4. Sagittal section. $\times 390$.
- " 7. A part of the right side of a polypide of a stage of development intermediate between those of Figs. 19 and 73. Seen from the sagittal plane. The cut surface lies to the right of the sagittal plane, and passes through the orifice of the right lophophore arm. The alimentary tract thus lies immediately above the plane of the paper. $\times 150$.

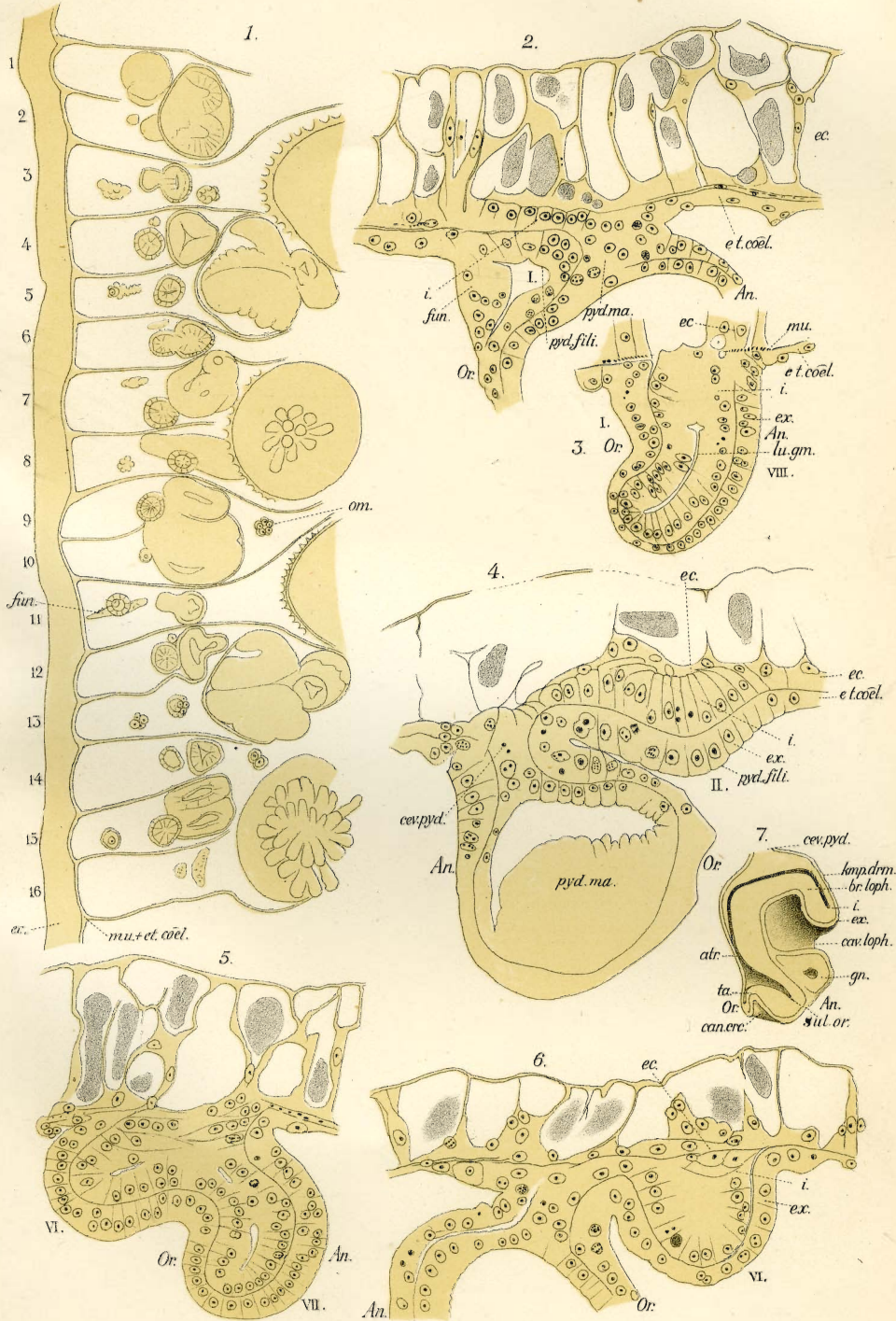


PLATE II.

All figures are magnified 390 diameters, and are from sagittal sections.

- Fig. 8. Stage II. in the same series as Fig. 2. The funiculus, *fun.*, has moved farther from the mother polypide. Margin to left.
- " 9. Stage IV. The inner layer, *i.*, of the bud is definitely formed, and the external layer is greatly thickened. Margin to left of figure.
- " 10. Stage V. The cells, *i.*, have arranged themselves in a layer, and begin to form an invagination. Margin to right.
- " 11. Stage VIII. The first indications of the alimentary tract appear as a depression in the inner layer, *rt.* The funiculus, *cl. fun.*, has begun to form, as is indicated by a disturbance of the cœlomic epithelium. Daughter bud forms Stage VI. in a series beginning with I, Fig. 3. Margin to left.
- " 12, 13. Successive stages in the formation of the alimentary tract.
- " 14. Stage VI. The two cell-layers are now definitely formed, and a lumen has begun to appear in the inner. Margin to right.
- " 15. Stage III. in the stoloniferous type of budding. Stolon has elongated greatly, and active cell division is taking place at its distal (i. e. marginal) end.

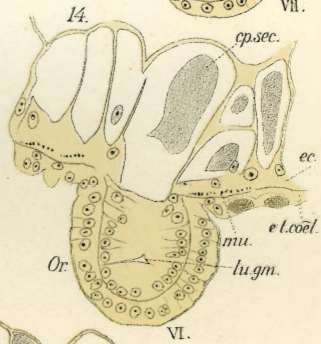
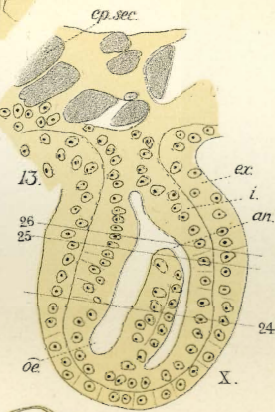
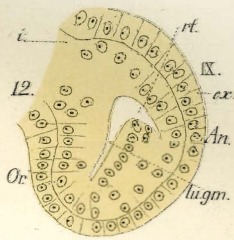
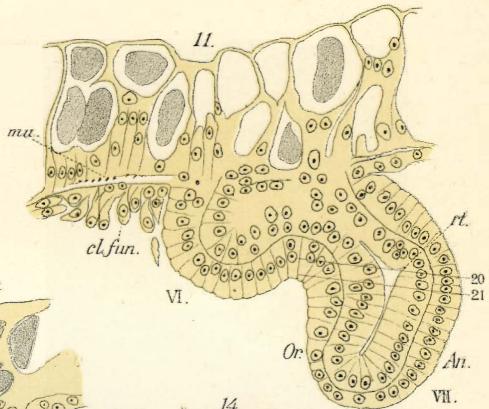
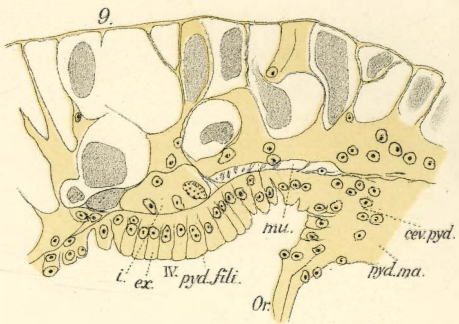
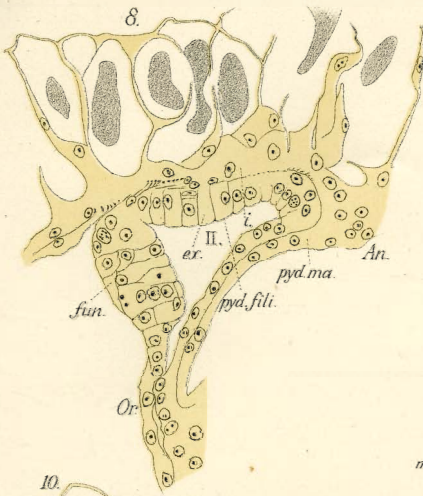


PLATE III.

All figures are magnified 390 diameters.

- Fig. 16. A later stage (VI.) in the *direct* type of bud formation. The mother polypide is cut to one side of its sagittal plane, and shows the invagination of the lophophore arm (*br. loph.*). The funiculus appears as scattered cells about both buds.
- " 17. A still later stage in the same series as Fig. 16. The daughter bud (VII.) has a lumen. In the mother polypide (XI.) the atrium has enlarged by the pushing of the lophophore arms. The œsophageal and rectal invaginations are not yet continuous, and the ring canal (*can. circ.*) has begun to appear oralward in the sagittal plane. Sagittal section.
- " 18. Stage XII. Alimentary tract nearly complete. Beginning of the formation of the ganglion. One of the lophophore arms is cut tangentially. Sagittal section.
- " 19. Stage XIII. Ganglion closing. The lophophore arm cut tangentially. Sagittal section.
- " 20 and 21. The positions and directions of the planes of these sections are shown by their projections on a sagittal section (Fig. 11, lines 20, 21) of an individual of the same age. To show non-participation of the outer layer in the first stage in formation of the alimentary tract.
- " 22. Early stage in *direct* bud-formation. Origin of funiculus, *cl. fun.* Sagittal. Margin to right.
- " 23. The position and direction of the plane of this section are shown by its projection on a sagittal section (Fig. 19, line 23) of an individual of the same age. This figure shows the folds of the inner layer at the mouth of the ganglionic sac.

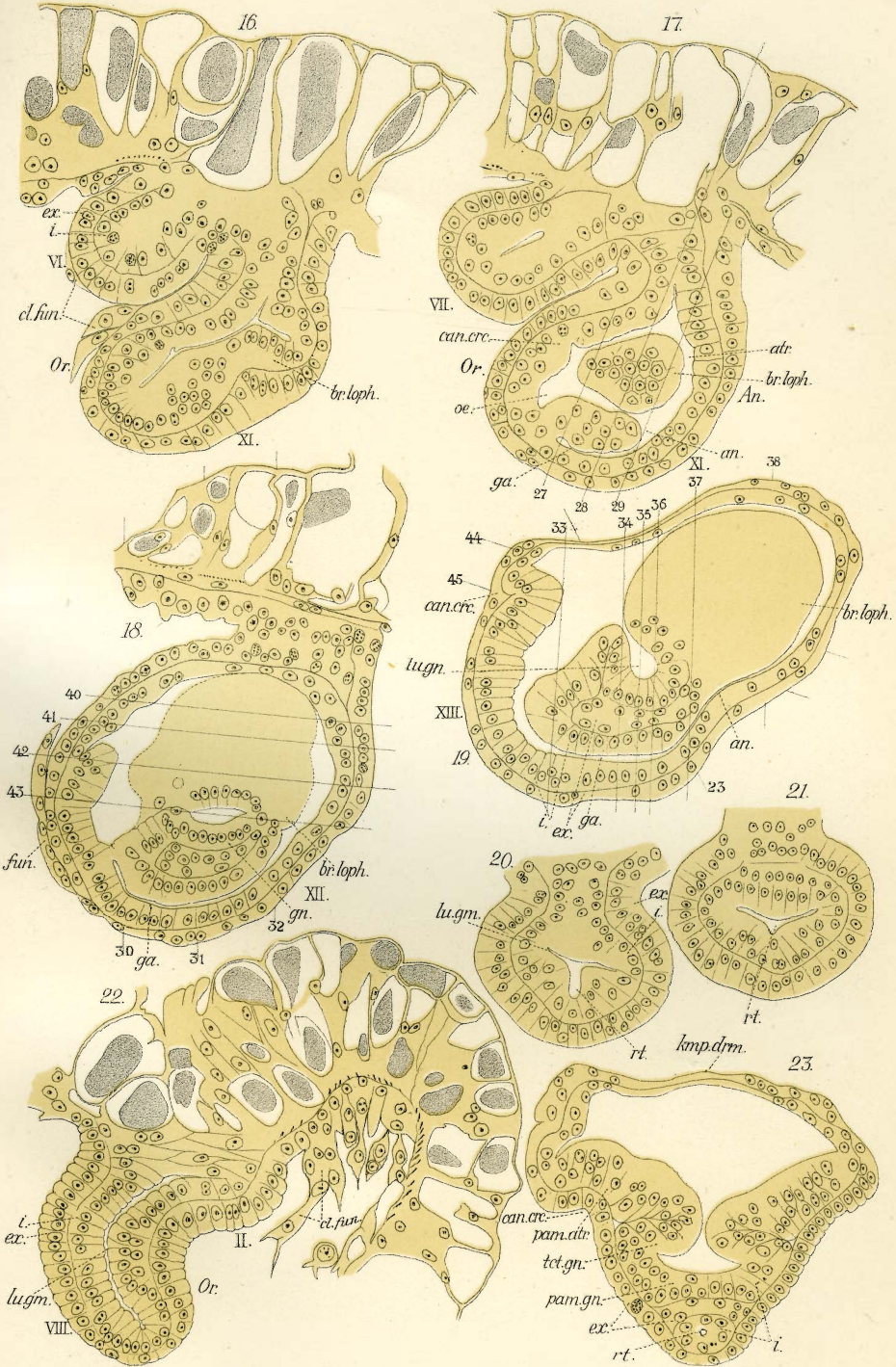


PLATE IV.

All figures, except Fig. 39, are vertical right-and-left sections, and all are magnified 390 diameters.

- Figs. 24-26. Three sections from a series passing from the oral to the aboral face of a polypide of about Stage X., and cutting it in the planes indicated by the lines 24-26, Fig. 13.
- " 27-29. Three sections of a series cut from a polypide of Stage XI. The planes of section are indicated in the lines 27-29, Fig. 17.
- " 30-32. Three sections, whose positions are indicated by the lines 30-32, Fig. 18, cut from a polypide of Stage XII.
- " 33-38. Six sections cut from a polypide of Stage XIII. in the directions indicated in Fig. 19 by the lines 33-38.
- " 39. A horizontal section of a polypide somewhat older than that represented in Fig. 18, and passing nearly in the direction of the line 43.

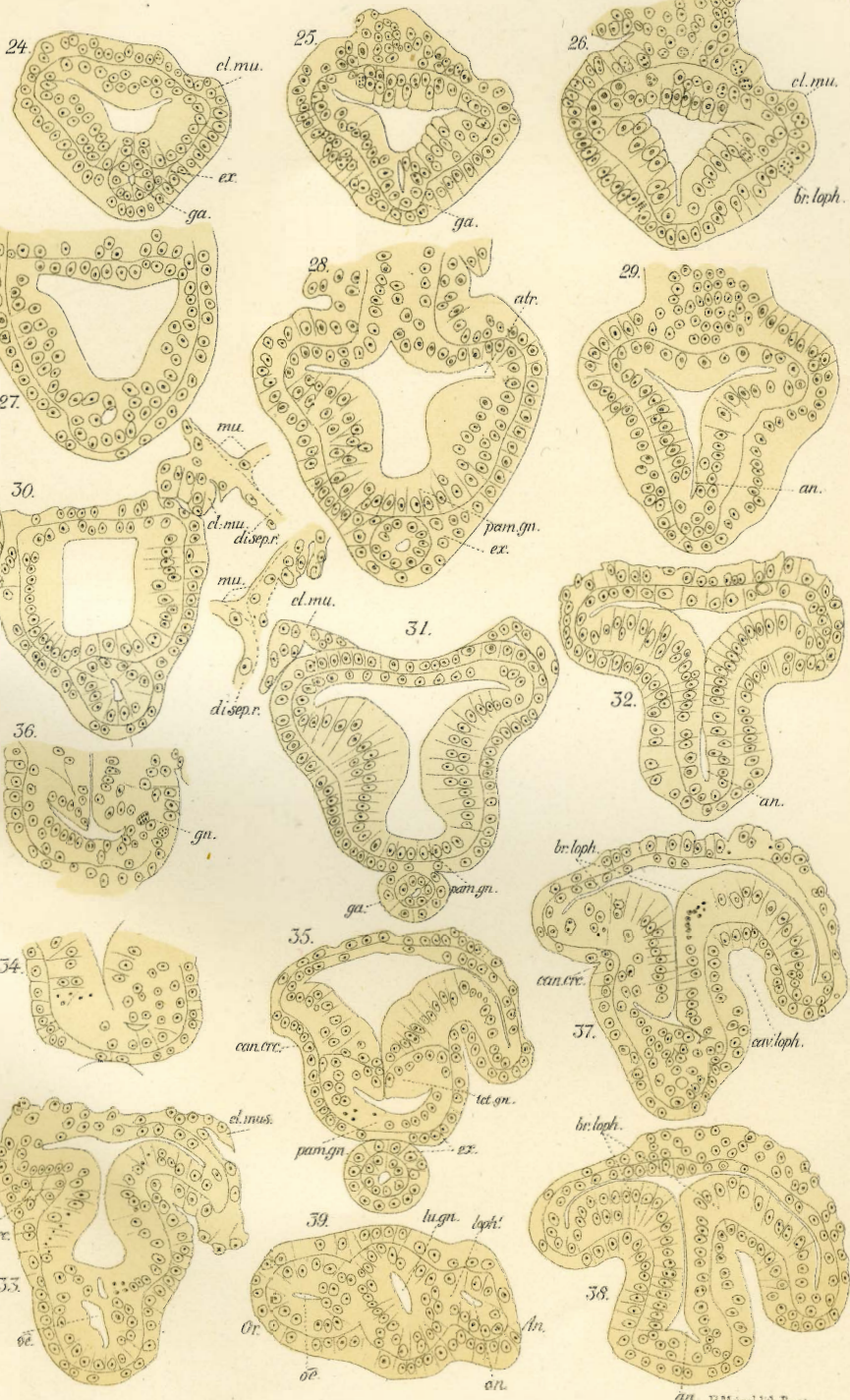


PLATE V.

- Figs. 40-43 are four horizontal sections of a polypide of Stage XII, passing in the direction indicated by the lines 40-43, Fig. 18. $\times 390$.
- " 44, 45 are horizontal sections of a polypide of Stage XIII. The direction of the cutting planes is indicated by the lines 44, 45, Fig. 19. $\times 390$.
- " 46-48. Sections through the migrating end of the funiculus, showing its relation to the cœlomic epithelium of the roof. The ectoderm is not shown. The arrow indicates direction of motion. $\times 390$.
- " 49. Transverse section through the funiculus, showing the loose migratory cells. $\times 390$.
- " 50, 51. Horizontal sections of a polypide slightly younger than Stage XIV., Fig. 73. Of these two sections, Fig. 50 is nearer the roof of the colony, and immediately above the ganglion. Fig. 51 is the second section below, and passes through the middle of the ganglion. $\times 390$.
- " 52. Sagittal section of the region about the brain of a polypide somewhat older than that shown in Fig. 77. This figure is reversed relatively to Fig. 77. $\times 600$.

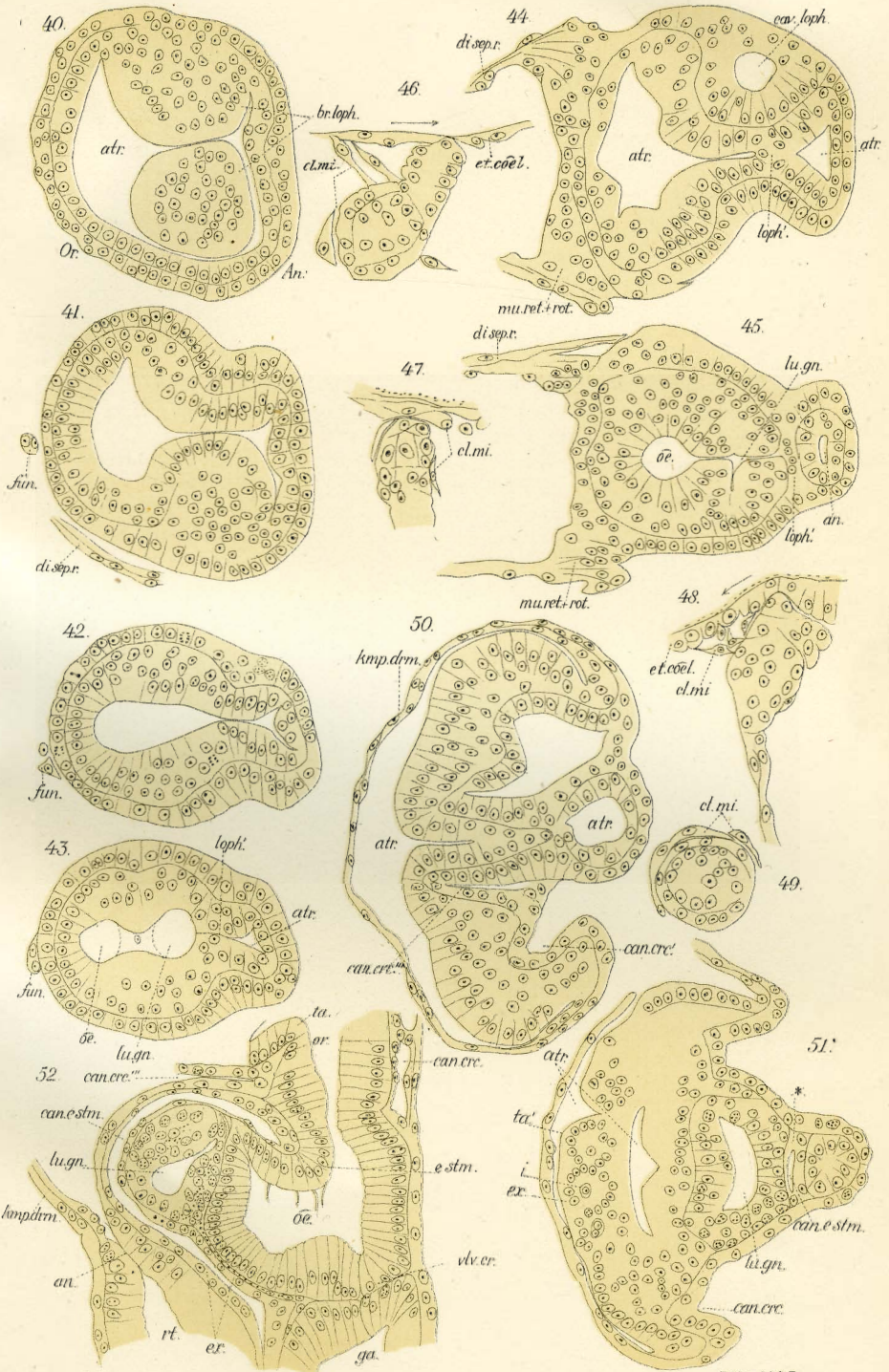


PLATE VI.

- Fig. 53. Young funiculus, showing its connection with polypide. $\times 390$.
- " 54. Origin of muscles. The section passes diagonally across a partition at the left, *di sep. r.*, and cuts the polypide tangentially at the right. $\times 390$.
- " 55. Section including a radial portion, showing the position of the muscles in the partition near the margin of the colony. $\times 390$.
- " 56. Section through the retractor and rotator muscles of a polypide of about the age of that shown in Fig. 77. $\times 390$.
- " 57. Young funiculus, whose upper end is free from the cœlomic epithelium of the roof of the colony. $\times 390$.
- " 58. Section through the sole, showing the relation between the muscle cells and the muscularis of the sole. $\times 600$.
- " 59. Section across a radial partition, and both rotator and retractor muscles which are migrating from the roof to the sole. $\times 390$.
- " 60. Section at right angles to the wall of the colony, showing the elongated and unmetamorphosed cells of the margin. $\times 390$.

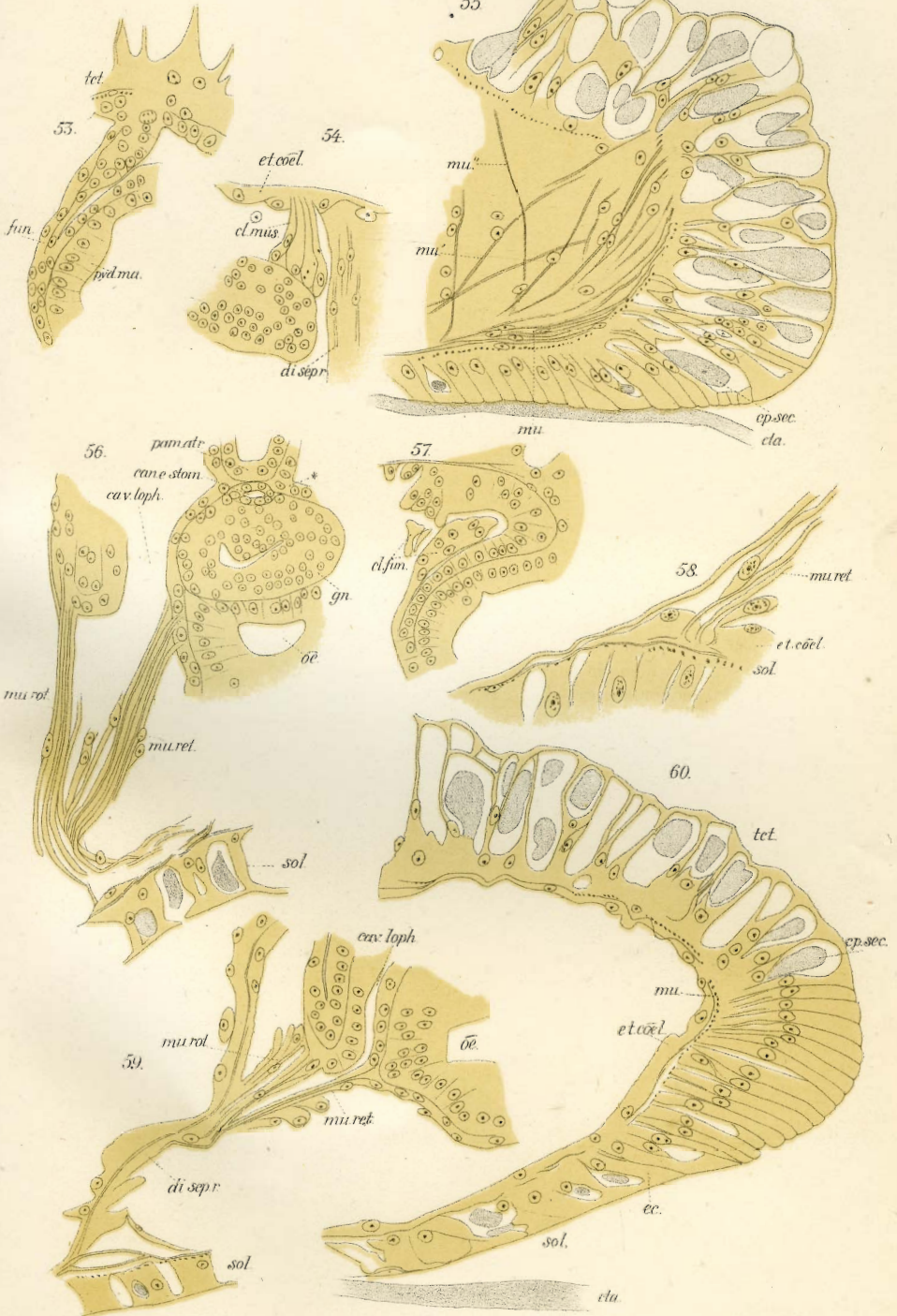


PLATE VII.

- Figs. 61-63. Three vertical right-and-left sections of same polypide passing from posterior end anteriorly. About Stage XIV. (Fig. 73, Plate VIII.)
× 390.
- “ 61. Section through lophophore arms, showing their fusion, *loph.*', and the position of the ring canal, *can. circ.*', *can. circ.*”
- “ 62. Section just posterior to anal opening, showing openings of lophophoric pockets.
- “ 63. Section through ganglion, showing early stage in formation of lophophoric nerve, parts of the ring canal, and young tentacles.
- “ 64. Cross section of lophophore arm, near termination of young nerve, at place marked 64, Fig. 71. × 1000.
- “ 65-67. Three successive sections through end of lophophore nerve in regions marked 65, 66, and 67, Fig. 71. These figures are from the same individual as Fig. 64, but from the opposite lophophore arm. × 1000.
- “ 68. Vertical right-and-left section through ganglion of an individual slightly younger than Fig. 63, showing origin of cornua by outgrowth of the walls of the ganglion, with an extension of the lumen of the latter. × 600.
- “ 69, 70. Longitudinal sections of two stages in the development of a tentacle, Fig. 70 being the younger. × 390.
- “ 71. Section through ganglion and growing lophophore nerve. Stage XIV. × 490.

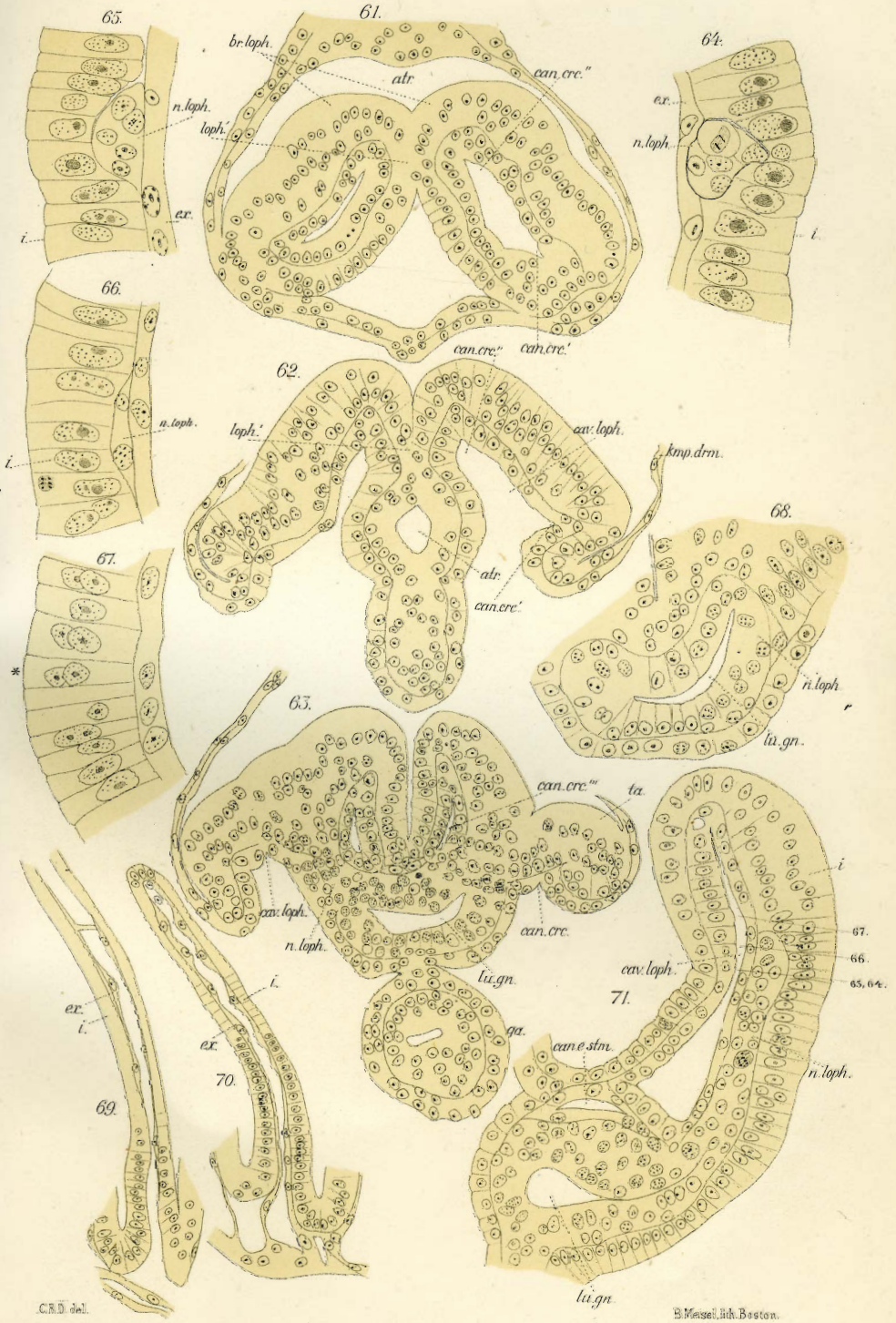


PLATE VIII.

- Fig. 72. Sagittal section of an adult polypide. The lophophore has been omitted. Outlines with camera lucida. Nuclei put in free hand. $\times 175$.
- “ 73. Sagittal section of bud. Stage XIV. The margin of colony to left. * Ectodermal cells derived from neck of polypide. $\times 390$.
- “ 74. Nearly horizontal section of a bud a little older than that shown in Fig. 73. The plane of section passes obliquely upward and forward. The tentacles are cut at different heights. $\times 390$.
- “ 75. Transverse section of lophophore arms before separation. The connecting band, *loph.*, is reduced to threads. The polypide has already evaginated. The section figured is the seventh from the distal end of the arms, — about 40μ distant. $\times 390$.
- “ 76. Transverse section of lophophore arms immediately after separation. The tentacles arising from *can. crc.*” were previously fused. $\times 390$.

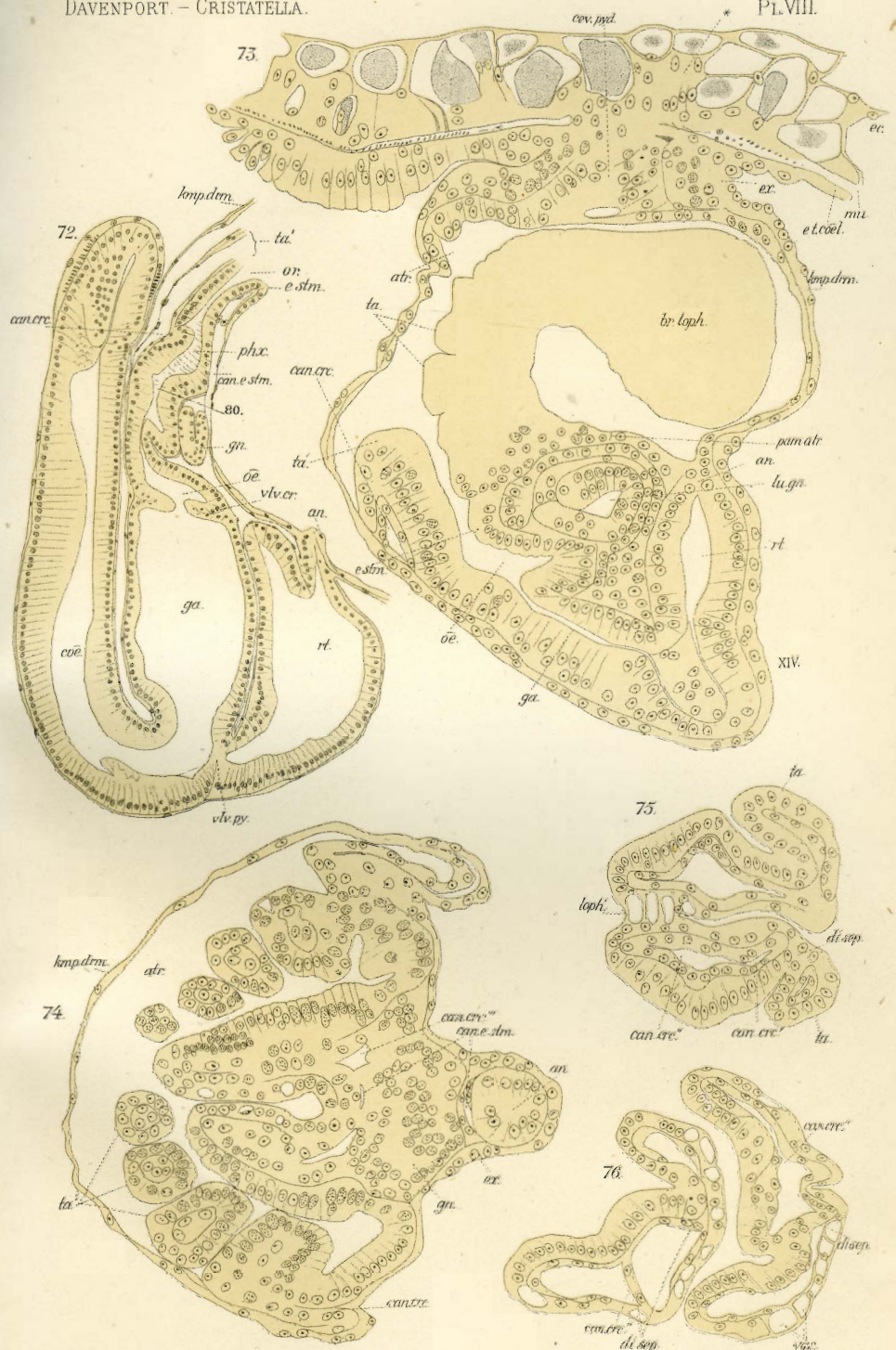


PLATE IX.

- Fig. 77. Sagittal section through a polypide, of which the atrial opening (*of. atr.*) has already begun to form. $\times 390$.
- “ 78. Horizontal section through the circumoral part of the ring canal, *can. crc.*, showing its free communication with the cœnocœl (*cœn.*). Adult. $\times 175$.
- “ 79. Vertical section through the roof of the colony (to the left) and the kamptoderm (to the right), showing their connection by the inferior parieto-vaginal muscles (*mu. inf.*) at an early stage of their development. $\times 600$.
- “ 80. Horizontal section in position marked 80, Fig. 72, Plate VIII, showing epistomic canal, *can. e. stni.*, and supra-ganglionic part of ring canal, *can. crc.*” $\times 390$.
- “ 81. Section cutting lophophore at base of tentacles. The arm of the right side only is shown entire. Stage of Fig. 77. $\times 175$.



PLATE X.

- Fig. 82. Transverse section of stomach of adult polypide. $\times 390$. Compare with Fig. 93.
- “ 83. Transverse section of proximal part of cœcum of same individual as that of Fig. 82. $\times 390$. Cf. Fig. 94.
- “ 84. Transverse section of œsophagus of a polypide whose atrial opening is just formed. $\times 390$.
- “ 85. Transverse section of the cœcum of an adult polypide near its distal extremity. $\times 390$.
- “ 86. Vertical section across a radial partition at its junction with colony-wall. $\times 600$.
- “ 87. Horizontal section of radial partition at its junction with colony-wall. $\times 600$.
- “ 88. Small colony of *Cristatella*, drawn from transparent object, showing polypides in optical section at different focal planes. \times circa 40.
- “ 89-92. Muscle fibres in successive stages of development. From thick sections. $\times 390$.
- “ 93. Transverse section of stomach of the same polypide as that from which Fig. 84 was taken; representing, therefore, a considerably younger stage than Fig. 82. $\times 390$.
- “ 94. Transverse section of cœcum of the same polypide as that from which Figs. 84 and 93 were taken, cut in a region nearly corresponding to the position of that shown in Fig. 83. $\times 390$.
- “ 95, 96. Two horizontal sections of a part of the margin of a small colony in which radial partitions are being rapidly formed in correspondence with rapid budding. Fig. 95 lies near the sole; Fig. 96, near the roof. The same figures refer to the same partition. $\times 300$.

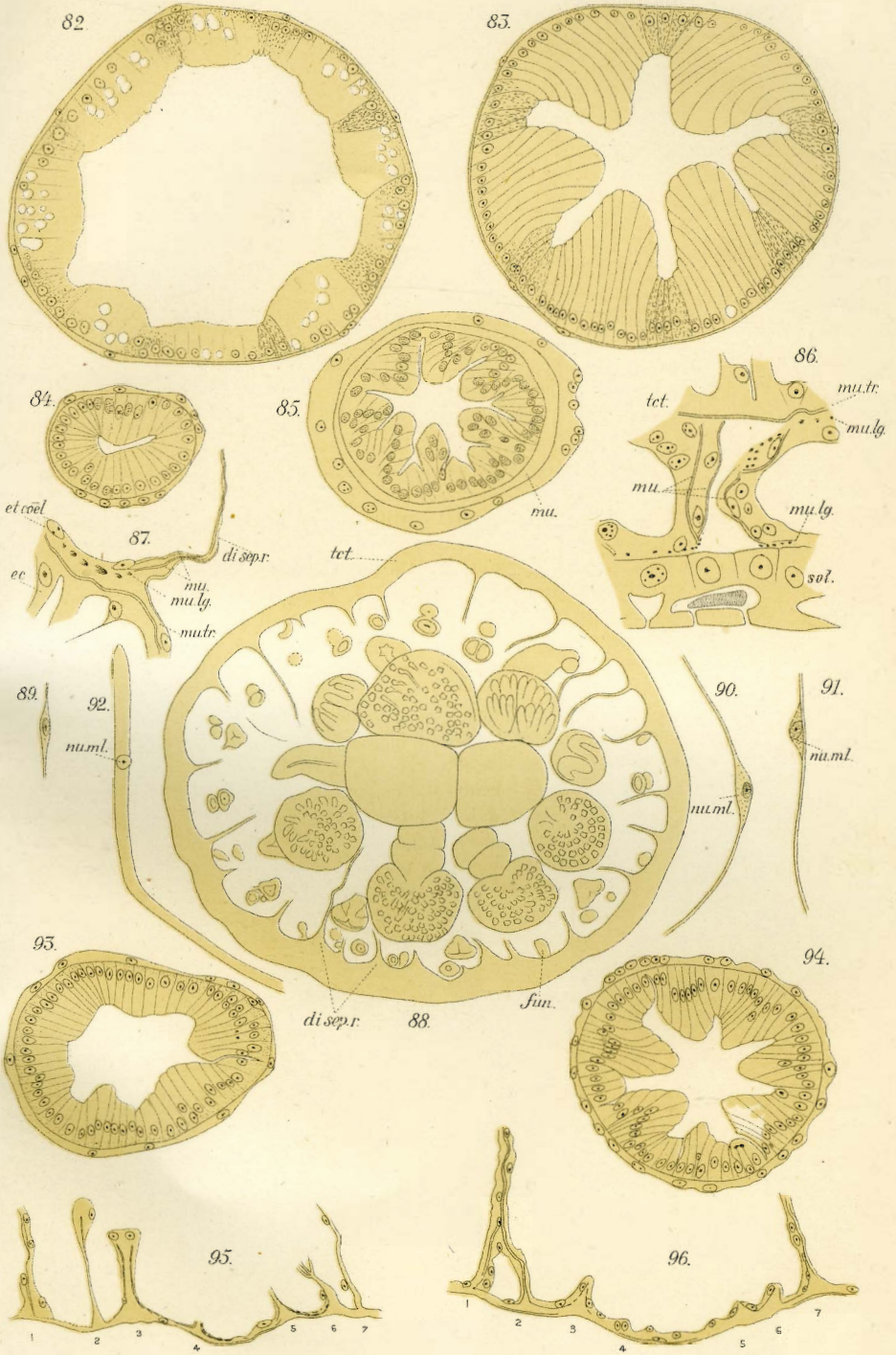


PLATE XI.

- Figs. 97-99. Vertical sections, showing three successive stages in the degeneration of the roof to form the atrial opening, *of. atr.*, and development of the parieto-vaginal muscles. $\times 390$.
- " 100. Late stage in the development of the ectoderm, showing its extreme modification between adult polypides. $\times 390$.

