No. 1. — *On Urnatella gracilis.* By C. B. Davenport.[1]

Contents.

I. Introduction.

In November, 1851, the late Dr. Leidy published, in the Proceedings of the Academy of Natural Sciences of Philadelphia, a notice of "what I suspect to be the cœnœcium of a new genus of Polyzoa; although I have never been able to detect the polypides if such exist." He gives three figures of the "cœnœcium," consisting of a series of urn-shaped segments placed so that the base of one segment rests on the mouth of its proximal neighbor. To this new genus he gives the name Urnatella, with a genus diagnosis, which three years later ('54, p. 191), after discovery of the polypide, was revised to read as follows : " Cœnœcium consisting of a series of segments up to eighteen in number, and forming free, semi-erect, curved stems, attached only by the base of the lowest segment. Segments excepting the three last ones simple, urniform ; the antepenultimate and the penultimate oblong, with simple or compound branches of the same form ; the last segment or active polyp is campanulate, and is supplied with cylindrical, ciliated arms arranged in a circle around the mouth." He finds that several stems arise from a common base. There are fourteen tentacles.

In 1856 Allman (pp. 117–119) referred to the discovery of Leidy, and published a pencil sketch of Urnatella furnished by Leidy. This is the

first published drawing of the calyx and young branches. Allman was inclined to refer this genus to the Pedicellinidæ.

In 1870 Leidy recorded further observations on Urnatella, and in 1884 he published in a thin quarto, with a single plate, everything which he had found out about its anatomy and physiology. The main points of these papers will be brought out in connection with the organs to which they refer.

Finally, Mr. Edward Potts, in a note to one of the editors of the American Naturalist (April, 1891), states that he has succeeded [as did Leidy] in obtaining in the spring rejuvenated heads from the headless stems of Urnatella gathered the preceding fall.

Various writers have called attention to the imperfections in our knowledge of this aberrant form. Ehlers ('90) has made many suggestions concerning the anatomy of Urnatella, which, being purely hypothetical, require to be settled by observation. Leidy himself was impressed with the importance of a better knowledge, and he had intended, he says ('84, p. 6), to make a thorough investigation of it. " Other occupations, and the want of a ready supply of the necessary material, have prevented my intention, and I am now led to communicate what I have learned of the animal with the view that some of my younger countrymen and co-laborers, under more favorable circumstances, may be induced to do what I had hoped and wished to do." To supplement the work of Professor Leidy is the object of the present paper, which has been largely inspired by his.

In 1884 Leidy remarked upon the absence of Urnatella from its former haunts. Apparently nothing had been seen of it since that time, until, in 1889, I opened correspondence with Mr. Edward Potts of Philadelphia upon the subject. In the summer of 1890 Mr. Potts and I thoroughly examined the waters of the Schuylkill River, both above and below the Fairmount dam, but without finding any trace of Urnatella. In September, 1891, Mr. Potts found many stocks in the bed of the temporarily emptied Schuylkill Canal, below Flat Rock dam, and kindly forwarded some of these, living, to me at Cambridge. In July, 1892, Mr. Potts and I re-examined in vain the Schuylkill River at Fairmount dam, and finally, on July 4, made dredgings in the Schuylkill at Flat Rock dam, near Shawmont Station, Pennsylvania. We found no trace of Urnatella in the quiet waters above the dam, but in the turbulent waters immediately below the overflow almost every stone brought from the bottom bore stocks, and some were almost completely covered on one face with luxuriant growths. One barrel-hoop dredged from the mud was

completely covered with headless stems. As many stones as we could carry were packed in moist paper or in jars, and transported safely several miles. A few days later, stones with living stocks of Urnatella and parts of the barrel-hoop with headless stems were transported in a pail of water to Cambridge. Upon arrival at Cambridge it was found that nearly all the heads had dropped off. The stocks were kept in running water for three months, during which time those which had lost their calyces did not regenerate them; whereas the stocks on the barrel-hoop did regenerate their heads, but did not bud very luxuriantly.

I cannot close this introduction without expressing thanks to my friend Mr. Potts, who, filled with love for the science, has unselfishly supplied me with material, hospitably received me into his household during my stay in Pennsylvania, and worked with me beyond his strength in our dredging operations on the Schuylkill in order to further a study of this animal.

The later studies included in this paper were made in the Embryological Laboratory, under the direction of Dr. E. L. Mark.

I propose to describe first the anatomy of the adult, and, in the second place, the non-sexual reproduction and regeneration, so far as I have been able to determine them. In each section of the paper I shall give first my own observations on Urnatella; secondly, compare them with those of others on Urnatella or other Endoprocta; and, finally, give my conclusions upon or interpretation of any difficult points.

II. ANATOMY.

For the purposes of description we must distinguish the stalk and the calyx.

1. *The Stalk.*

The stalk is an elongated, filamentous structure, composed of a number of segments, lying one beyond the other. The number of such segments varies from one to several, according to the age of the stalk. Leidy counted as many as eighteen. I have never counted more. Looked at with a hand lens, the stem is seen to be composed of alternating translucent and opaque rings, of which the former occupy the middle zone of each segment; the latter have an intersegmental position. The surface of the stalk in the translucent zone is thrown into circular folds, and small processes appear scattered over its surface, more abundantly on the more distal segments (Plate I. Fig. 6).

An optical longitudinal section of the living stalk (Plate I. Fig. 7) shows that it consists of a thick cuticula, within which is a mass of ill-defined tissue. The cuticula is thicker and more opaque in the basal segments, thinner and more transparent in the distal ones. Each of the basal segments often contains a mass of globular, highly refractive bodies, which may be forced out from the segment by crushing the latter (Plate I. Figs. 4, 5). Isolated by this means they are seen to be of the most varied size, and to resemble yolk spherules. Besides these granules, one finds lying near the cuticula in all but the oldest segments a fibrillated layer consisting of elongated, spindle-shaped, highly granular cells in the midst of the yolk spherules (Plate I. Fig. 7), and, finally, one or several flickering bodies reminding one by their motion of the *cirri*[1] of flame cells. In the dark zones optical sections reveal indications of a transverse septum.

A more accurate insight into the histological structures is gained from thin sections of the stalk.

The *cuticula* appears in two conditions, which are not sharply separated, but pass into each other through intermediate conditions. The one kind (Plate I. Fig. 4, *cta.*) occurs in the middle zone of each segment. It is transparent and flexible, and becomes thicker in passing from the distal to the proximal segments. It stains in hæmatoxylin, and is then seen to be composed of laminæ, for it appears in section distinctly striated (Plate I. Fig. 4 ; Plate II. Fig. 16). The other kind of cuticula occurs chiefly at the constrictions between segments, but it extends over the two ends of the segments also, and even over the middle zones of the segments, as an outer cuticula (Plate II. Fig. 8, *cta'.*). It forms, moreover, the septa between adjacent segments. It does not stain in hæmatoxylin, is more highly refractive than the first kind, and has a yellowish color by transmitted light. Where it passes over into the first mentioned kind of cuticula, it becomes distinctly striated, and gradually loses its specific characters, gaining those of the first kind, of which it is probably only a modification. It is the presence of these two kinds of cuticula that causes the superficial appearance of alternating light and dark zones on the stem. These two kinds of cuticula do not correspond to the inner and outer cuticulas which Ehlers ('90, pp. 16, 17) describes for Ascopodaria. Two layers with the characters of those of Ehlers appear not to exist in Urnatella.

The *ectoderm* (Plate II. Figs. 11, 10, 16) diminishes in thickness from

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[1] I employ the word "cirrus" in the sense in which it is used by Bütschli for Ciliata (cf. Bronn's Thierreich, Protozoa, p. 1324).

the distal end of the stalk, where it is a layer of cuboidal cells, to the base, where its cells are extremely flattened, so that the layer is hardly distinguishable. Even near the base of the stalk, however, the ectoderm is a relatively thick layer on each of the surfaces of the transverse septa.

The *axial portion* of the stalk presents very interesting histological conditions. In a young individual whose stalk comprises a single segment only (Plate II. Fig. 15) the axial portion contains a closely packed mass of cells, which stain deeply, contain few vacuoles, and are slightly elongated in the direction of the axis of the stalk. At a later stage one finds the plasma of some of these cells undergoing a metamorphosis. Such cells appear filled by a vacuole in which lie numerous highly refractive granules. A little later all of the axial cells have become greatly elongated in correspondence with the elongation of the stalk. Many of them appear almost completely vacuolated. A cross section of the stalk at such a stage of development is shown in Plate II. Figure 9, where the centre is filled with a network of cell boundaries enclosing clear spaces. This condition is very striking in longitudinal sections through the region of the septum, where the long vacuolated cells may be seen extending from one segment into the other.

According to Ehlers ('90, pp. 18–22), the stolon of Ascopodaria shows a condition of the axial portion similar to that here described ; but in the stalks which support the calyces there is a considerable amount of intercellular substance, and I find the same thing in Pedicellina. In Urnatella, on the contrary, such intercellular substance appears only in the older stalks.

The *musculature* of the adult stalk is situated immediately within the ectoderm, and is found in all segments running from one septum to the other. On cross section of the stalk it appears as a circle of radially elongated, highly refractive bodies, placed close to the ectoderm (Plate II. Fig. 9, *mu*). Each elongated body has, at a certain focus, a darker periphery and a lighter central line. With the highest powers the darker periphery can be resolved into a single row of bodies, which appear as bright spots at the highest, as dark spots at the lowest focus (Plate II. Fig. 16, *mu*). These I interpret as fibrillæ.

The fibrillæ develop in the protoplasm of the axial cells. In their earliest stages one sees them forming a single row on the outer edges of the more peripheral cells (Plate II. Fig. 17, *mu*). Later they are formed on the two lateral edges also (Fig. 11). Additional lateral (or, in relation to the stalk, radial) rows of fibrillæ are next formed in each cell, the new rows appearing nearer the centre of the cell than those already

formed (Fig. 10). Finally, in the adult, the nucleus of the cell, which has been pushed centripetad by the multiplication of fibrillæ, comes to lie opposite several pairs of radial rows or sheets of fibrillæ. These sheets always occur in pairs, the components of the pairs being separated by a narrow clear space, and the pairs by broader spaces.

As I have said, this musculature occurs throughout the entire stalk up to the base of the calyx (Plate III. Fig. 19, *mu.*). I do not understand on what ground Ehlers states ('90, p. 146) that in Urnatella "der Muskelmantel in den gleichmässig dicken Stengelgliedern nicht deren ganze Länge erfüllt."

There is a considerable difference between my description of the structures of the muscle fibres and that of Ehlers ('90, pp. 25–28) for Ascopodaria. In the latter case, the muscle cells are placed three to five deep, instead of in one peripheral series, as in Urnatella. Moreover, in Ascopodaria the fibrillæ lie in two thick peripheral bands on the sides of each muscle cell ; whereas in Urnatella several muscle bands (each consisting of a single row of fibrillæ) belong to each cell.

The differences between the two genera are easily explained by assuming an increase in the number of muscle cells in Ascopodaria, so that they can no longer lie in a single peripheral series, and that the fibrillæ bands have become greatly crowded together, so that one band is not equivalent to a single band of Urnatella, but to all of the bands of Urnatella which have arisen on one side of the cell. The stalk musculature of Ascopodaria is thus more highly developed than that of Urnatella.

Ehlers mentions the resemblance between the muscle fibres of Ascopodaria and those of Nematodes, especially the Cœlomyaria.

I have referred above to vibratile movements in the living .stalk. Stained sections show, placed more or less abundantly throughout the stalk, elongated spaces terminating blindly at one end in structures which must be regarded as flame cells (Plate II. Fig. 12, *cl. flm.*). Such a flame cell is spherical in form, stains slightly, possesses a large nucleus, and gives off into the elongated space *cl. tb.* the well known cirrus (*Wimperflamme*).

The form of the cirrus in all cases examined was conical, the axis of the cone being usually thrown into a sigmoid curve. Where the cirrus arises from the cell, it is slightly constricted, then enlarges suddenly, forming a thickened ring. Distal of this ring the cirrus tapers gradually to a fine point. That the cirrus is composed of a number of agglutinated cilia is indicated by the presence of longitudinal striæ. I believe that the flame cell closes the lumen of the tubule at this point.

Concerning the space into which the free end of the cirrus projects I can only conclude, from comparison with other cases where a flame cell occurs, that this must represent the lumen of an excretory tubule. I have not, however, been able in any instance to trace an individual tubule to any considerable distance, or until it opens into any other organ. One thing seems fairly certain, there is no morphological difference between those elongated clear spaces into which the cirri project and the elongated vacuolated cells to which reference has already been made. I am therefore inclined to regard it as probable that they are one and the same thing. The vacuolated cells are developed by the breaking down of the plasma of the elongated cells of the young stalk. Before the metamorphosis is completed, one finds cells filled with clear contents, in which lie scattered granules (Plate II. Fig. 15, cl. tb. left). Finally, even these seem to disappear (Fig. 15, cl. tb. right). Since the tubules agree in size with these elongated, later vacuolated cells, I conclude that their lumina are intracellular. Since the so called vacuolated cells — many of which at least are, according to my view, tubules — pass uninterruptedly from one segment to the next through the central opening of the septa, there may easily exist continuous tubules running from the basal segments into the calyx.

The only excretory tubules which have been heretofore mentioned as occurring in Endoprocta are the pair which lie in the calyx and open into the atrium between mouth and rectum. Farther on, I shall have occasion to inquire into the probable significance of the facts here recorded.

In specimens of Urnatella gathered in the fall and examined while living, I found the basal segments filled with yolk granules (Plate I. Fig. 4). Even in stocks collected in July, the basal segments contained a greater or less amount of yolk. In passing from the distal towards the proximal end of the stalk, one can trace the development of this yolk, and since this is a matter of some general interest I have paid a little attention to it.

If we examine one of the middle segments of a stem whose basal segment is full of large yolk spherules, we shall find reserve stuff forming in some of the elongated cells. It appears as a fine granulation throughout the whole cell, except immediately surrounding the nucleus (Plate II. Fig. 13). Not all of the cells appear thus granular, for others are at this stage vacuolated. Still later (Fig. 14) many of the fine granules appear to have fused into larger ones, and these are separated by clear spaces. The cells have enlarged very greatly (those

in Figs. 13 and 14 being equally magnified), and their boundaries seem to be at some points discontinuous. Finally, in the basal segment we find all trace of cell boundaries lost, and the central space filled by a mass of large and small yolk globules, nuclei, and protoplasmic débris (Plate II. Fig. 8).

The series of stages in the formation of yolk, which are shown in successive segments of the same stalk, points to the conclusion that yolk is in this case formed inside of the cell by a fusion of many excessively small granules, — a conclusion similar to that reached by Stuhlmann ('87, p. 23) for the eggs of a Teleost. Hand in hand with the development of yolk there seems to go a diminution in the amount of protoplasm, which therefore seems to be broken down in the process. The details of this process resemble remarkably those of the formation of the yolk in the statoblast of Phylactolæma, for an accurate description of which we are especially indebted to Braem ('90, p. 76).

Urnatella is quite unique, so far as I know, among all Endoprocta in the storage of food material in its stalk. This is doubtless of high physiological importance, as I shall try to show later.

Septa occur at the constrictions between segments, and separate the latter from one another. They are composed of a circular fold of ectoderm, whose free edge surrounds a small opening, through which spindle-shaped vacuolated mesenchymatous cells pass. The adult condition is easily interpreted by reference to the development, an early stage in which is shown in Figure 24 (Plate IV.). Between the layers of the ectodermal fold a perforated disc of cuticula — continuous at its outer edge with the superficial cuticula — becomes laid down. This cuticular disc increases in thickness with increasing age.

The most distal septum, which separates stalk and calyx, is more complicated than the others. The complication is due to the fact that mesenchymatous cells have placed themselves in and above the opening of the septum, and have flattened themselves out perpendicularly to the axis of the stalk, while still allowing the vacuolated cells to pass at their margins into the calyx from the stalk. Thus the transversely flattened mesenchymatous cells appear to send out horizontal processes between the tubular cells (Plate IV. Fig. 25).

The flattened cells which lie above the opening of the septum are seen, in longitudinal section of the stalk, to be arched over the opening. It results from this that the smaller, lower cells lie partly enclosed by the larger upper ones (Plate III. Fig. 18).

A septum between stalk and calyx agreeing even in detail with that

just described for Urnatella has been described and figured by Ehlers for Ascopodaria. Such a highly complicated septum seems indeed to be common to the Pedicellinidæ, which in this respect appear more nearly allied to Urnatella than does Loxosoma, in which such septa are absent.

In Pedicellina Benedeni also, which has a segmented stalk, the segments are separated from one another, according to Fœttinger ('87, pp. 301–303), by perforated septa.

2. *The Calyx.*

Under this heading I shall treat successively of the body wall (including the lip of the atrium, and the tentacles), the atrium, the alimentary tract, the body cavity, the nephridia, the sexual organs, and the nervous system.

A good idea of the external form of the expanded calyx may be gained from Leidy's figures. My own, having been drawn chiefly from preserved material, show the polypide for the most part in a retracted condition (cf. Plate I. Fig. 2). When thus retracted, the atrial opening does not lie at the apex of the calyx, but is thrown sharply over towards the oral aspect (Plate III. Fig 18).

The body wall is composed of a single layer of excessively thin epithelium, — the ectoderm, — which has secreted a thin cuticula. This cuticula is thickened in places, producing papillæ, which are irregularly scattered over the calyx. At the lip of the atrial opening, as the passage into the atrium in the retracted condition may be called, the ectoderm is thicker than elsewhere, and folds back upon itself until it reaches the base of the lophophore. This backward-reflected portion I shall call by the name *kamptoderm*, for although its homology with the kamptoderm of Ectoprocta may not be entirely beyond doubt, I cannot see any important difference between the two structures, either in their adult relations or in development. As in the Ectoprocta, so here the polypide is formed in the retracted state, and the atrial opening does not break through until a late stage is reached.

In Ectoprocta the line of union of the kamptoderm and body wall, i. e. the lip of the atrial opening, is marked by a thickened ring composed of elongated ectodermal cells, at the base of which lie the fibres of a sphincter muscle. This organ constitutes the "Randwulst" of Phylactolæmata or the "Diaphragma" of Gymnolæmata. Does an organ homologous with this occur in Urnatella? It is in keeping with the more primitive organization of the Endoprocta that, although a corre-

sponding region exists and sphincter muscles are found here, it has not become so distinctly differentiated from the rest of the body wall as has the *Randwulst* of Phylactolæmata. This region may be designated the lip of the atrium.

When the tentacles are expanded, — a secondary condition, as the development of the calyx shows, — the lip of the atrium forms a circular ridge lying at the base of the tentacles (Plate IV. Fig. 26, *spht. atr.*). When the tentacles are drawn in tightly, the lip of the atrium becomes puckered. Two of the folds resulting from this process are shown cut across in Figure 19 (Plate III.) above the middle of the atrium.

The *tentacles* of Urnatella in three cases in which I counted them on transverse sections, as well as on the entire animal, numbered twelve; in one case, thirteen. In addition to these numbers, Leidy ('84, p. 10) found sixteen (usually) and fourteen. In the specimen with thirteen tentacles, the odd one was placed on the anal aspect of the calyx in the median plane. It appeared shorter than the others. In one case with twelve tentacles, observed fully expanded, the two tentacles of the anal aspect lying nearest the median plane appeared shorter than the remaining ones. Leidy does not refer to this point, and his figures afford no satisfactory evidence as to the occurrence of this condition in his specimens.

The tentacles are each composed of a cylinder of columnar epithelium surrounding a narrow central region which is filled with mesenchymatous tissue. In addition, on each of the lateral aspects of the tentacle there is a muscle, composed of one to three fibres lying side by side (Plate IV. Fig. 27, *mu. ret. ta.*). The epithelium is ciliated on the lateral and inner faces of the tentacle.

The *atrium* is bounded by the tentacular corona on all sides. The floor of the atrium passes into the mouth in the oral region, and rests upon the rectum in the aboral region. At the centre there opens into it an elongated pocket, the cloaca. The lateral angles of the mouth are prolonged aborally, and form two grooves which open into the atrium along the lateral margins of the floor (Plate III. Fig. 19, *sul. atr.*). These, which may be called the *atrial grooves*, approach each other and become shallower as they pass aborally upon the atrial wall, until they disappear in the median line above the rectum. The epithelium lining the grooves is ciliated.

This "atrial groove" exists also in Pedicellina echinata according to Nitsche ('69, pp. 21, 22), and, according to Ehlers ('90, pp. 52, 53, 59, 60), in his Ascopodaria macropus also. Its function, as has been fre-

quently pointed out, must be to carry the particles of food from the bases of the tentacles towards the mouth.

The mouth is limited on the side towards the anus, and separated from the cloaca by a fold, which may be designated the *inner lip*. This represents the organ often referred to as the epistome, — a term which implies an homology with the organ of the same name in Phylactolæmata. This organ is of greatest size in Rhabdopleura and Loxosoma among Endoprocta, where it is elevated far above the general level of the floor of the atrium. It is less marked in the Pedicellinidæ. In Urnatella it is not at all evident, because its upper edge is not higher than the roof of the rectum which forms the actual floor of the atrium behind. If, on the contrary, the cloaca extended underneath the rectum, as it does in the Pedicellinidæ, causing a great space between it and the intestine, and thus making the roof of the *intestine* the floor of the atrium, the inner lip would appear as a very prominent organ (cf. Fig. 18).

On the outer edge of the mouth, and forming the " outer lip," is a prominent horizontal fold of the oral part of the atrium (Fig. 18, *loph. atr.*). This fold extends aborally, running parallel with, and forming the outer wall of the " atrial groove " (Fig. 19). The fold gradually becomes less pronounced towards the aboral aspect of the atrium until (in Fig. 18) it forms only a slight swelling of the atrial wall over the rectum.

Alimentary Tract. — As in other Endoprocta, so in Urnatella one can distinguish four regions in the alimentary tract : œsophagus, stomach, intestine, and rectum. The wall of the alimentary tract is composed throughout of a ciliated epithelium, except in the so called hepatic cells of the upper wall of the stomach. In this exception Urnatella agrees with other Pedicellinidæ, but for Loxosoma Harmer makes no such exception.

I find a highly refractive basement membrane lying at the base of the digestive epithelium. This stains deeply in hæmatoxylin, so that it can be seen with a low power as a distinct line surrounding the alimentary tract. Such a condition, described by Nitsche ('69, p. 19) for Pedicellina, has been denied by Ehlers ('90, p. 72) to exist in Ascopodaria.

There is an indication of a specialized intestinal (sphincter) muscle surrounding the opening leading from intestine to rectum, as well as at the anus. The structure in question, which appears in section (Fig. 18, *spht.*) as highly refractive and deeply staining areas on either side of the opening, seems to lie in the epithelial wall of the alimentary tract.

Since elsewhere in the calyx of Urnatella, and in other Bryozoa, muscles arise from mesodermal tissue, I am inclined to believe that, notwithstanding their position, they are formed from mesenchymatous cells which have crowded in between the epithelial cells.

The free surfaces of the epithelial cells are different in the various regions of the alimentary tract. On the wall of the œsophagus they run out into tolerably close-set and long cilia, which become longer towards the deep end of the œsophagus, and project into the stomach at its cardiac end (Fig. 18, œ.). Along the lateral and lower sides of the stomach one finds longer sparsely distributed cilia, and at their base a close-set layer of short rods (Stäbchen). Around the pyloric opening of the stomach there is a ring of elongated cilia. The intestinal epithelium bears chiefly short, stout, and close-set *Stäbchen*. The cilia of the rectum are confined to the upper wall, and are of medium length, and sparse. These are omitted in Figure 18.

The position of the mouth has been already defined. It leads into a broad *œsophagus*, constantly narrowing as it descends until it opens into the stomach at the lower (oral) end of the latter. Its wall consists of a columnar epithelium, some of whose cells are vacuolated, especially at the base of the epistome. The inner wall of the œsophageo-gastric opening is provided with a valve-like process, covered, like the opposite wall, with large cilia.

The pear-shaped stomach is lined below and laterally by a cuboidal or short columnar epithelium, above by a highly granular, more or less vacuolated, non-ciliated epithelium, whose free ends are ragged, sending processes into the lumen of the organ. These constitute the so called hepatic cells. Their granules stain deeply in hæmatoxylin. In the epithelium of the lateral and lower walls of the stomach deeply staining cells alternate irregularly with less deeply staining ones (Fig. 18). These cells are also full of small vacuoles.

The stomach is separated from the intestine by a circular ridge, formed of elongated cells bearing long cilia, — the pyloric valve.

The cells of the conical intestine are cuboidal, and possess a thick external and internal membrane, which stains deeply in hæmatoxylin. The passage into the rectum is restricted.

The epithelium of the rectum is composed of flattened cells. Its lower wall is closely applied to the upper wall of the intestine, the two walls being separated by the basement membranes of the two cell layers.

The anus lies, as already stated, on the aboral wall of the cloaca. At this point the wall of the rectum becomes continuous with the floor of

the atrium above and the aboral wall of the cloaca below. The cells surrounding the anal opening are slightly larger than their neighbors. Lying apparently in the basement membrane is the anal sphincter already mentioned.

Under the term *body cavity* I include the space lying between the alimentary tract and the outer body wall and atrium. This space, which is much reduced in the retracted condition of the polypide, contains indifferent mesenchymatous tissue, tubular cells, muscles, the excretory and sexual organs, and the nervous system.

The body cavity is bounded by no other epithelium than the ectoderm of the body wall and atrium, and the entoderm of the alimentary tract; that is to say, there is no mesoderm.

The indifferent mesenchymatous cells have been seen to best advantage in the end of a regenerating stalk shown in Figure 3. Here the cells, which were studied while living, could be seen migrating on the inner surface of the ectoderm, and extending through the central region. Such wandering cells were filled with highly refractive granules.

The tubular cells of the body cavity lie chiefly at the base of the calyx, near its attachment to the stalk. In this region also I have seen in the living animal a flickering ciliate movement, and in the sectioned animal flame cells.

I have been able to distinguish only two systems of muscles in the body cavity of Urnatella, — the sphincter of the atrium, and the muscles of the tentacles.

The sphincter of the atrial opening (Plate III. Fig. 18, Plate IV. Fig. 26, *spht. atr.*) is composed of circular fibres lying in the lip of the atrium. Taken together, the fibres form a folded sheet, U-shaped on cross section, the convexity of the U being directed upwards. The function of this muscle is, of course, to constrict the atrial opening, and thus to protect the tentacles and parts below.

The tentacular muscles consist of the pair to each tentacle already mentioned. These run from the apex of the tentacle to the base, where they diverge to the right and to the left, and, after breaking up into many branches, pass through the ectoderm to become inserted upon the cuticula of the body wall. Leidy ('84, p. 10) saw these tentacular muscles.

Differentiated muscles do not seem to be abundant in the calyx of any of the Endoprocta. Tentacular muscles are unknown in other species. On the other hand, Ehlers ('90, pp. 64, 65) has described two systems for Ascopodaria which I have not seen in Urnatella, namely, lateral

wall muscles and transverse muscles, the latter running from the right to the left wall. The fibres of these muscles also break up into branches before making their attachments.

Excretory Organs. — The chief excretory apparatus in Urnatella lies in the calyx below the ectodermal floor of the atrium (Plate III. Fig. 18, Plate IV. Fig. 22, *nph.*). It consists of a pair of tubules which unite proximally and open by a single pore into an unpaired cavity, which in turn opens into the atrial chamber at about the centre of its floor. This unpaired cavity is the one I have proposed to call the *cloaca.*

From its opening into the cloaca the unpaired tract of the excretory tubules, which may be designated *efferent duct,* runs oralwards and downwards, and then divides, the two tubules following the posterior wall of the œsophagus. Finally, the tubules turn back upon themselves, running outward and towards the rectum. The whole excretory apparatus has thus the form of the Greek letter Υ.

Each tubule ends blindly in a flame cell which bears the characteristic cirrus, exactly similar to that found in the stalk (page 6). Figure 22 (Plate IV.) shows the end of the tubule of the left side. The plane of this section was such that it cut the posteriorly reflected region of the excretory tubule of the left side throughout all but the middle of its extent. At the middle line the tubules of both sides sink below the plane of the section, so that it is the efferent duct which is cut at *nph.* in the median plane.

One of the youngest individuals in which I have found a nephridium is that from which the section Figure 29 (Plate IV.) was drawn. The efferent duct (*neph.*) appears to be composed of two elongated cells placed end to end. Running through the midst of these is a poorly marked lumen, partly filled by a granular substance. This and one or two other similar cases seem to me to support strongly the view of the intracellular nature of the lumen of the nephridium.

The evidence derived from the adult condition is less satisfactory, but points to the same conclusion. Thus one finds on cross section of the tubules that the lumen is not sharply limited like the exterior of the tubule. In fact, one sometimes finds delicate threads traversing the lumen (Plate III. Fig. 21, *a–c*). In one of these sections two nuclei are cut across, which in so far militates against my conclusion that the lumen runs inside of single cells placed end to end. But I believe these to be the nuclei of two adjacent *overlapping* cells.

On account of the evidence just presented, I regard the nephridium of Urnatella as having an intracellular lumen and ending blindly in a

flame cell, and am thus brought into complete agreement with the results obtained by Harmer from Loxosoma. His conclusion ('85, p. 279) that the Endoproct. nephridium is probably to be regarded as a head kidney, like that of Trochophores, seems to me to be justified. A further discussion of this topic must be deferred till towards the close of this paper.

The nephridium opens, as already stated, not directly into the vestibule, but into a pocket of it, the *cloaca* (Plate III. Fig. 18, Plate IV. Fig. 28). The wall of the cloaca consists of a layer of cuboidal epithelium which is perforated by three openings, — the anus, and the proximal openings of the efferent duct and of the vas deferens.

The cloaca is an organ which does not occur in any other Endoproct. Its existence here is due to the unique position of the rectum and anus, and of the opening to the vas deferens. In Loxosoma the last is very far removed from the opening of the nephridia. In the Pedicellinidœ the two openings are less distant from each other. In the male of P. Benedeni (Fœttinger, '87, Plate X. Fig. 16), the anus and the openings of the nephridium and vas deferens are quite near together; but in the female the oviduct of that species opens far distant from the other organs.

Sexual Organs. — Curiously enough, I have not found among all the individuals sectioned any ripe females. All the mature individuals of the lot collected by me on July 4th from the Schuylkill appear to have been males. In no individual did I notice any difference in the position of the ducts, such as obtains between the two sexes in Pedicellina Benedeni, — no trace of an incubatory chamber between rectum and the floor of the vestibule.

In the male organs two parts may be distinguished, — testis and vas deferens. The testis (Plate IV. Fig. 23) is a paired ovoid body lying between rectum, intestine, and the floor of the atrium. In the figure given one observes spermatozoa in various stages of development, the wall of the sac constituting the germinative epithelium.

The vas deferens (Plate III. Fig. 18, Plate IV. Fig. 28) is an unpaired U-shaped tube, the concavity of the U being turned oralwards. The wall consists of a cuboidal epithelium which is ciliated, at least at the proximal end of the tube.

The vas deferens of Urnatella resembles in form that of P. Benedeni (Foettinger, '87, Plate X. Fig. 15), which in turn seems to be more complicated than that of Ascopodaria.

Nervous System. — I have been able to make only a superficial study of this system. The main ganglion (Plate III. Fig. 18, Plate IV. Figs.

22, 29, *gn.*) lies between vas deferens and nephridium, is elongated transversely, and slightly constricted in the median plane. One can distinguish a central region composed of fine fibres running transversely, and a cortical region of cuboidal, deeply staining cells with large clear nuclei. I have not succeeded in tracing any peripheral fibres from this ganglionic mass, as Ehlers has done in another Endoproct.

III. Non-sexual Reproduction.

1. *Architecture of the Stock.*

Urnatella forms stocks by budding. As in other Bryozoa, the buds are normally produced in a very regular manner. I believe that I have determined the law in part, although it has exceptions, as the law of budding in every Bryozoan stock has. As Leidy has stated, several vertical stalks may arise from the same horizontal plate. A single stalk may remain unbranched, giving rise to new individuals at its distal end only, or it may give rise to branches which come off irregularly from a few segments. Usually only one branch arises from a single segment, but occasionally two do so (Plate V. Figs. 35, 38).

The length of these branches and the number of their segments decrease towards the distal end of the main stalk, and the conclusion seems justified that it is only at the distal end that they are formed. Excepting for these occasional branches, the lower segments of the stalk are bare of any branches or polypides. The distal end, however, is usually crowded with polypides so thickly as to make it difficult to count them or to determine their points of attachment (cf. Plate V. Fig. 30).

A very casual observation, however, shows that the buds from the main stalk are of two kinds; first, those which have given rise to a linear series of segments at the distal end of which is a calyx, and these are what I have called *branches ;* and, secondly, those consisting of a *stolon*-like process, from one surface of which arise calyces resting upon a stalk of usually one segment only. The surface of the stolon upon which such polypides are placed is a definite one, namely, that which is turned towards the distal end of the main stalk. The budded branches and also the stolons are grouped upon the oral side of the adult stalk.

In the clearest cases, in young or not too richly branched stocks, I find the branch arising on the oral surface of the segment, and between two stolons, which are therefore more nearly lateral (Plate V. Figs. 37, 38, 40, 42).

One may therefore say that *usually the branches are median and oral, the stolons lateral.* Again, the branches give rise, like the primary stalk, to two kinds of buds, branches and stolons. The stolons give rise only to stalks of one segment each, bearing a calyx distally. These calyces are so placed that their oral surface is directed towards the distal end of the stolon. I have not found more than two individuals borne upon a stolon.

I have previously ('91, p. 72) tried to show how all buds in the stocks of Bryozoa are to be referred back to embryonic tissue lying at the tips or margin. In Endoprocta, however, the extreme tips seem to be occupied by a polypide, and the embryonic tissue lies in a zone at the base of the latter. This difference may be regarded, however, as only apparent, and the two conditions harmonized by conceiving the polypide in Endoprocta retracted into the stalk, below the zone of embryonic tissue, — the condition realized in Ectoprocta. The distal part of the stalk will then become terminal, constituting an apical ring of embryonic tissue surrounding the secondary atrial opening thus produced. From the oral portion of this ring new buds — branches and stolons — are, as in Plumatella, proliferated; and this process is repeated for each segment. At (or near) the apices of these incipient branches and stolons lies a mass of embryonic tissue which gives rise in the one case — branches — to the stalk, the polypide, and the *Anlage* of new buds; and in the other — incipient stolons — to the stolon and the *Anlage* of the individuals which bud forth from it. The differences between the branch and the stolon are, however, more apparent than real, as a comparison of the diagrams Figures 59 and 60 (Plate VI.) will make clear. In one case (Fig. 59) the mass of embryonic cells in any segment does not grow out far beyond the youngest individual produced from it; in the other case (Fig. 60) there is a considerable growth beyond the youngest individual. Thus in the latter case a long stolon is produced, in the former it remains at a minimum.

As I have already stated, in most cases, particularly in young vigorous stocks, one meets with the condition which may fairly be called typical, in which from one segment three buds — one median (branch) and two lateral (stolons) — arise. This typical condition may be expressed by the formula on the next page.

This formula will be understood by reference to the diagrams on Plate VI., of which it is a symbolic expression. The letters represent in all cases calyx-bearing individuals, the asterisks gemmiparous tissue. The capital A stands for the individual which forms the main stem under

consideration. The ✻ immediately below it represents the embryonic mass situated at the tip of the stalk, from which all the gemmiparous tissue distributed throughout the stock has taken its origin. As the stalk has grown, there have been left behind the embryonic masses represented by ✳. Three of these have arisen together, and the process has been repeated as often as segments have been formed. The separation of the segments is represented in the formula by a dash. Between every two dashes the same budding process is repeated.

```
                        A
                        ✻

                *       *       *
                    _____

          -    ✳ x a     a     a x ✳
                         x
                         ✳
                    _____

                x               x
      ✳ x b    x x a     a     a x x    b x ✳
                x               x
                    x    x    x
                         b
                         x
                         ✻
```
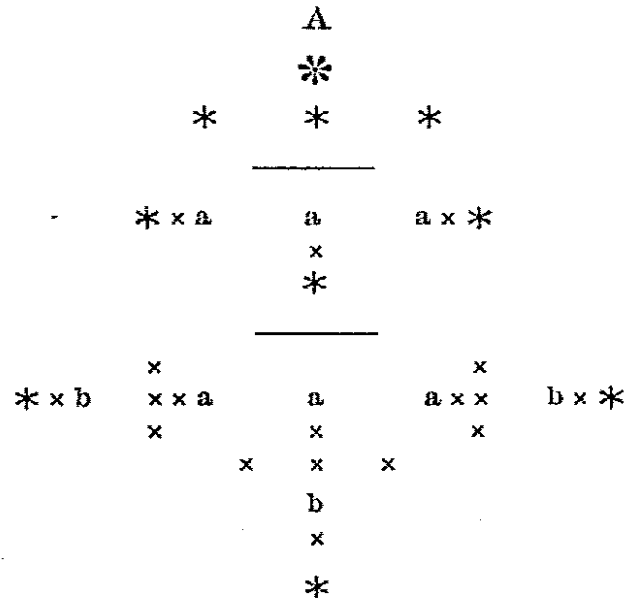
The median embryonic masses (✳) give rise to the individuals a, b, and c, and leave with each a dowry of embryonic tissue represented by x. Each of these individuals a, b, and c, with its embryonic mass x, now acts exactly like A ✻. The lateral embryonic masses act precisely as do the median ones.

The typical condition expressed by the foregoing formula is not often perfectly realized, for the simple reason that the stock would thereby become too crowded. The more frequent modifications are the absence of the median bud, the absence of one or both of the lateral buds (stolons) and, occasionally, the apparent substitution of a branch for a stolon.

The foregoing formula is one of the most complicated that it is necessary to make for Bryozoa, for nowhere else are the embryonic masses so abundant relative to the polypides, or, in other words, nowhere else are so many embryonic masses borne by one individual. It is quite common among other species to find three embryonic masses arising from one; but here the formation of triple masses is repeated as often as the number of segments in the stalk. This fact raises the question of the significance of these segments, and leads us to discuss the subject.

2. Segmentation of the Stalk.

Leidy ('84, p. 9) did not fail to call particular attention to the division of the stalk of Urnatella into segments, and recognized their successive production " through the process of division, very much in the same manner as in the production of the proglottides of tape-worms from a scolex."

The phenomena of segmentation must have a special interest on account of the relation of segmentation and strobilization. I shall treat under this subject, first, of the phenomena of segmentation in Urnatella; secondly, of the probable origin and significance of the process in this genus; and, thirdly, I shall examine critically Leidy's comparison.

The transverse septum, which is the first indication of the separation of the stalk into segments, begins to be formed at about the time that the lateral buds arise, and immediately below them. It arises, as already stated (page 8), as a ring-like fold of the ectoderm, whose free edge encloses a circular orifice, through which the interiors of the two segments which are being formed are continuous (Plate IV. Fig. 24). By continued growth of this fold the diameter of the orifice diminishes, never wholly closing, but leaving a space for the passage of the tubular cells, to which reference has already been made (page 7). In this process the sheath of longitudinal muscles, which originally ran immediately inside of the ectoderm continuously from the base of the calyx to the last fully formed septum, becomes discontinuous at the place of the ingrowing fold, and the separated ends of the muscle fibres become attached to their respective faces of the septum.

In order to discover the significance of this process of segmentation we must first study its distribution throughout the Endoprocta. Usually the calyx is borne upon an unsegmented stalk. Such is the condition, for example, in Loxosoma, Pedicellina echinata, P. Americana, and Ascopodaria. In other cases, Gonopodaria (Ehlers, '90, p. 146) and P. Belgica (Fœttinger, '87, p. 301), there is a poorly expressed and highly variable segmented condition. In Arthropodaria (Pedicellina) Benedeni the stalk is distinctly and regularly segmented, there being partitions and slight external constrictions. Finally, in Urnatella we find the segmented condition still more sharply expressed.

There is a suggestive parallelism between the formation of segments and the production of buds. While with one exception all species with unsegmented stalks produce no buds, and none have yet been described

as occurring on Gonopodaria and P. Belgica, budding does occur to a slight extent on Arthropodaria, and still more profusely on Urnatella. There is one genus, however, Barentsia (Vigilius, '84a, p. 86), which buds sparsely and has an unsegmented stalk. Here, however, as in Urnatella (Plate VI. Fig. 58) and Arthropodaria (?), there is a septum between the branches and the main stalk.

Finally, in all Pedicellinidæ which have been studied carefully there is a septum between the stalk and calyx.

One may bring these scattered facts of distribution of the septum into some sort of unity by saying that in the Pedicellinidæ every calyx and every lateral branch (where such exists) is partly cut off from communication with the interior of the mother stalk by septa. This is effected by the production of these organs at the place of junction of the calyx and the lateral buds to the stalk, and in some cases also by the partial division of the stalk itself into compartments by septa. The transverse septa must have either a morphological or a physiological significance. They might be regarded as a part of the wall of zoœcia, equivalent to the zoœcia of Paludicella, and therefore to be morphologically equivalent to the septa of Paludicella. On this hypothesis each segment of the stalk of Urnatella would be an (incomplete) individual. The idea of the individuality of the segments would seem to be sustained by the fact that each gives rise to similar buds, and that apparently any segment has the capacity of regenerating the lost calyx, or end of the primary stalk. On the other hand, dissepiments might be regarded as structures which had grown across the originally unsegmented stem to fulfil some need of the organism. Comparative anatomical studies seem to me to favor the second view. In Loxosoma, and in most marine Pedicellinidæ, we find a stalk without dissepiments. In other forms dissepiments are few and variable in number, in still others they are constant in occurrence, and from the segments arise buds. Finally, in Urnatella, the segments are separated by the dissepiments, each becomes more individualized, and has the capacity of giving rise to buds having the same arrangement. The differentiation of the separate segments has gone so far that one can hardly see in the stalk of Urnatella, resembling a string of beads, the assumed smooth cylindrical stem of its Pedicellina-like ancestors.

If we seek for an explanation of the dissepiments, I think it is to be found in the protection of the stock against the influx of water and destroying organisms at the time of the loss of calyx or lateral branches, which would make regeneration impossible. This is the same hypothe-

sis which I offered in a former paper ('91, p. 40) to account for the formation of a septum in Ectoprocta.

In favor of this hypothesis are not merely the need of such an apparatus on account of the frequent loss of the calyx and the lateral branches through accident, and the fitness of this mechanism for the function, but also the existence of the special mechanism of radiate cells, covering over the opening in the dissepiment between the calyx and stalk, — a dissepiment which will be most useful in the manner indicated by this hypothesis, owing to the delicacy of the calyx and its liability to accident. When the lateral branches or the terminal calyx become detached from the parent stem, we find that the pore in the septum, remaining behind as a part of the wall of the stalk, has become sealed by a cuticular plug. So also Ehlers ('90, p. 22) in Ascopodaria. In this case we can see the utility of the dissepiment, and can infer its value in those positions where it is not certain, but only possible, that it may be called into play. My conclusion then is, that the dissepiments have a purely physiological meaning, possessing a protective function, and that the segments of the stem are only physiological divisions of a primitively undivided stalk, which have perhaps no other significance than that they are parts separated by the dissepiments.[1]

It follows naturally from the foregoing hypothesis, that the segmentation of the stalk has succeeded, rather than preceded, the condition of bud formation from the stalk, it being rendered desirable owing to the greater danger to mutilation to which the stalk is exposed. From this standpoint we can see why buds should be produced on each segment in a similar manner. The relative profuseness of budding in Urnatella is explainable on other grounds.

Examining more closely the relation of this process to the production of proglottides in a tape-worm, — accepting the view that the production of proglottides is fundamentally a process of continual regeneration of lost parts, — there seems to be an important difference in this, that the growth of the stock of Urnatella is limited, more than ten or twelve segments being rarely formed, while an indefinite number of proglottides are produced. The limited growth of the Urnatella stem seems to indicate that the production of segments is not the production of new parts,

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[1] Freely branching stocks of Hydroids have septa interpolated at the base of the hydranth, which is peculiarly liable to fall off, and sometimes in the middle of the stems. The occurrence of such similar structures throughout the two most profusely branching groups of Metazoa is further evidence for the validity of the physiological explanation of them which I have offered.

but the division, progressing towards the calyx, of an originally simple stalk into a number of parts, — that the growth of the Urnatella stalk is limited just as that of the Pedicellina stock is limited, and for the same reason.

3. *Orientation of the Individuals.*

The orientation of the individuals of the stock seems to be here, as in Ectoprocta, a very definite one. In Pedicellina and its close allies, as well as in Urnatella, the young individuals budded from the parent stalk face the same way as the polypide of the parent stock. Seeliger ('90, p. 571) has pointed out that in all the species of Loxosoma the orientation of the buds with reference to the parent is definite, but different from that found in Pedicellina. The orientation of the buds in Loxosoma (which arise, as in Pedicellina, on the oral side of the mother) is the reverse of that of the mother. Thus it comes about that the oral aspect of the buds in the Pedicellinidæ is turned towards the periphery of the stock, that of Loxosoma towards the centre. This is the same difference which has been found to prevail between the buds of Phylactolæmata and Gymnolæmata, and as in this case, so in Endoprocta the differences may be harmonized by a different method of expression. *In all Endoprocta the oral aspect of the buds is turned towards the centre of proliferation.* For in Loxosoma new individuals are produced between the next older and the parent stock, the centre of proliferation remaining in the parent stock, while in Pedicellina it migrates away upon the end of the stolon. The typical condition in Loxosoma is represented by the formula

$$a \qquad b \qquad c \qquad d \quad * \quad A \,;$$

that of Pedicellina by

$$* \quad d \qquad c \qquad b \qquad a \quad A,$$

in which the asterisks represent gemmiparous tissue.

The general statement of the relation of the aspects of the buds to the proliferating region is the reverse of that which I have given for Ectoprocta ('91, p. 82), which reads, " In both Phylactolæmata and Gymnolæmata, the *anal* aspect is turned towards the gemmiparous region." It is important to note, however, that this difference corresponds to a difference in respect to the part of the alimentary tract which is formed by the principal pocket of the atrium, for this in Ectoprocta gives rise to the posterior part of the elementary tract ; in Endoprocta, on the contrary, to the anterior part. The differences in the process of budding in

the two groups can be harmonized, and at the same time the physiological nature of the differences indicated, by putting the statement thus : — In all Bryozoa, the formation of the alimentary tract begins at that end which is turned towards the gemmiparous region (cf. page 28).

The problem of the difference in the method of development of the alimentary tract in Ectoprocta and Endoprocta, is the same as that of the differences in the development of the alimentary tract of Triploblastica in general.

As is well known, the midgut in Triploblastica is produced by an invagination whose mouth — the blastopore — comes to be in some cases at the anterior part of the tract, in others at its posterior part. This variation in the method of formation has been explained by the hypothesis that the blastopore represents the opening into the gastro-vascular cavity of Cœlenterates, which is functionally both mouth and anus ; and that as we find a physiological separation of the opening in many Cœlenterates, so a morphological separation of the gastrula-opening into mouth and anus by concrescence of the lips of the blastopore in the mid-oral line, has occurred in the ontogeny of Triploblastica. In some cases both mouth and anus arise by this process, in other cases only one organ, the other arising secondarily, or (preferably) later. The part which arises later might be regarded as a new formation, or, following Caldwell ('85, p. 23), as derived from a part of the entoderm which had become separated from the greater part in the separation of the two extremities of the elongated lip of the blastopore to permit the placing of mouth and anus at opposite poles of an elongated animal.

The application of these facts and their explanations to the facts of the formation of the alimentary tract in the Bryozoan polypide is evident. Gastrulation takes place not in the act of first invagination of the inner layer of the bud, but in a secondary invagination from the bottom of the first formed sac. The blastopore does not lie on the surface of the body wall, but has been carried below the surface, and its position is indicated by the plane of separation of alimentary tract and atrium, where the roof of the gut and the floor of the atrium have been produced[1] by concrescence of the lips of the blastopore. The atrium then is in no way lined by entoderm; it is merely a precociously developed, protecting pocket of the body wall, which occurs in that region in which invagination of the entoderm is to take place. The primary atrial opening is not at all the blastopore, as some authors have called it.

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[1] Compare Seeliger, '89a, pp. 181, 182; so also in Paludicella, see my earlier paper, '91, p. 19, and probably in Phylactolæmata, cf. Kræpelin, '92, p. 33.

My conception of the relation of the processes of atrium formation and gastrulation will be more easily understood if we compare the formation of the polypide with the early stages in the development of the egg of Sipunculus, as given by Hatschek ('83, pp. 78–81). Here gastrulation occurs only in the depths of the invagination at the vegetative pole ; the more superficial part of the cavity is the trunk amniotic cavity. This corresponds to the atrium of Bryozoa, and, like it, is lined by ectoderm.

The concrescence of the lips of the blastopore takes place slightly differently in Endoprocta and Ectoprocta, so that in one case the blasto-pore persists in the region of the permanent mouth, and the procto-dæum appears later ; whereas in the other case the blastopore persists in the region of the permanent anus, and the stomadæum arises later.

In all Bryozoa, however, the main ganglion arises in the region of con-crescence, precisely as the ventral nerve cord is now known to do in most invertebrates. Thus additional support is given to the idea that the ganglion of Bryozoa is a *subœsophageal* one.

4. Histology of the Buds.

The *histological structure* of the branches is exactly like that of the parent stalk. The minute structure of the stolons deserves a word of description. The base from which the individuals arise is filled with mesenchymatous cells, which at the distal, growing end are closely packed and deeply stainable (Plate VI. Figs. 51, 57, *sto.*). Some of the cells are differentiated into muscle fibres, which run up into the stalks of the individuals that have arisen from the stolon (Fig. 57, *mu.*). The epithelium at the distal end of the stolon is composed of cuboidal or slightly elongated cells. At the base of the stolon the epithelial cells are greatly elongated and closely packed together (Figs. 51, 57, *cl. sec.*).

At the point of attachment to the parent stem the stolon is consider-ably constricted, the epithelium forming an inward fold surrounding a small opening through which the parenchymatous tissue of the bud and the mother stalk are continuous (Plate VI. Fig. 58, *di. sep.*). Between the layers of this circular fold is secreted a cuticular disk, perforated at its centre.

5. Formation of New Stocks.

The development of Urnatella from the egg has never been seen, and I was naturally anxious to get embryological material. On looking over my preserved material I found no trace of eggs, although there were many ripe males. I have no direct knowledge, therefore, as to whether

I was too early or too late for embryological material, although from some indirect evidence drawn from what follows I am inclined to think I was too early.

The youngest stocks found I obtained in large numbers, and they were of almost exactly the same age. Moreover, they agreed with the youngest stages found by Leidy and figured by him ('84, Plate I. Figs. 5, 6, 7). I have represented some of these in Plate V. Figures 31, 32, and, enlarged, in Plate II. Figure 15, and Plate V. Figure 46.

I have already (pages 3–6) called attention to some of the characters of the stalks of these young individuals. It remains to mention the "basal plate" of such stocks.

Unlike its condition in the adult, the "basal plate" is a relatively large organ of elongated cylindrical form (Plate II. Fig. 15). Its outer epithelium consists of sharply demarked cells, cuboidal above, columnar below. This epithelium has given rise to a cuticula thin and dense above, and thicker and less refractive below. The columnar cells are somewhat less deeply stained than those at the end of the "basal plate" farthest from the two stalks. Their nuclei lie at their inner ends. The outer part of the cell contains spherical masses of granules. On the whole, it stains less deeply than the inner end. Finally, one always finds particles of dirt closely adherent to the under and lateral aspects of the basal plate.

These facts I interpret as follows. The columnar cells of the under side are glandular, and secrete a sticky substance which causes the adherence of the surrounding particles of dirt, and thus serves to *anchor* the young stock.[1] The tissue of the interior of the "basal plate" is remarkable, and difficult of interpretation from sections alone. In such sections one sees bands running through the middle region and crossing at various angles. Each of these "bands" is a nucleated cell, and probably represents a muscle fibre (cf. Plate V. Fig. 46). One sees also fibres having a different appearance running radially from the base of the stalk to the columnar cells of the "basal disc" over quite a long stretch (Plate II. Fig. 15). In addition to these protoplasmic structures there are long clear spaces which are bounded by thin membranes and contain occa-

[1] Seeliger ('90, p. 573) finds in Pedicellina a glandular differentiated zone on the base of the stolon, where it comes in contact with foreign bodies. This, he says, can be traced unbroken through the entire length, especially in young stocks, consisting of few individuals. The foot gland of Loxosoma is an organ fulfilling a function similar to that of the glandular cells of the stolon, but an homology of the two organs can hardly be maintained.

sional nuclei. These are the tubular cells already referred to. Some of them contain the agglutinated cilia characteristic of flame cells, and they arise from large cells, which must indicate the beginnings of the excretory tubules of the stalk already mentioned.

What is the meaning of the fact that no younger stages than these occur, although such and all older stages are abundant? Have these young stocks been derived from fertilized eggs, or have they some other origin?

I have already referred to the fact that the great mass of the buds of any Urnatella stock are found at the upper end of the parent stalk. The lower and middle parts of the stalk possess few buds, although they once constituted the upper end of the stalk. What has become of the buds which have been lost? Leidy asked this question, and the facts led him "to suspect that the branches are spontaneously and habitually detached from the parent stem, to become elsewhere attached, and thus form new colonies." I have evidence that raises the suspicion of Leidy to as near certainty as can be obtained by use of the morphological method. *The "youngest stocks" are derived from the stolons of the parent stalk, which habitually become free for the purpose of founding new stocks.*

To establish this proposition it will be necessary to show, (1) identity of structure between old lateral buds and young stocks, and (2) the scar of attachment of the young stock to the parent stalk (cf. Plate VI. Fig. 58). Of identity of structure there can be no question. Often it would have been quite impossible to distinguish between young stocks and "stolons" which had been violently broken off from the parent stalk and were lying loose in the bottle, were it not for a single criterion, namely, the young stocks had dirt adhering to their lower surface. An application of the second criterion leads to the same positive result. In series of thin sections of young stocks one can always find at one side of the median plane the scar of former attachment, which appears as a thickening of the cuticula into which ectodermal cells may sometimes be seen penetrating (Plate V. Fig. 47). We have here, then, a method of non-sexual propagation quite similar to that obtaining in Loxosoma, where the buds habitually drop off, so that this genus is commonly said not to be stock-producing. This resemblance must be regarded as being purely a physiological one, and not in the least implying any closer relationship of the two genera.

I have already expressed my belief that the stolons are thrown off regularly *for the purpose* of founding new stocks. On this assumption we can account for the rapid growth of the embryonic tissue giving rise to a

stolon-like body, which will become a basis of support for the new stock, the "basal plate." One can thus account for the thickened cells of the under side of the stolon, which appear before detachment (Plate VI. Figs. 51, 57). The question remains, Do the median branches play a similar *rôle* to the stolons? I do not think they do, for the reasons, (1) that, having no basal plate, they are not physiologically fit for forming new stocks; (2) that I have found no new young stocks having one parent stem with one or two generations of budded individuals, — the condition of the median branches ; (3) that, on the contrary, one often finds such median branches persisting on even the lower segments of the stock. (Plate V. Figs. 35, 39, 40. Compare Leidy, '84, pp. 8, 9, Plate I. Fig. 4.) Since the median branches frequently persist as a part of the parent stock, — they are not produced in the first place on every segment, — I conceive their function to be the increase of the number of proliferating points in the stock itself.

Starting with the young stock, one can find all stages of growth up to the most complicated conditions (Plate V. Figs. 33, 36, 43, 44). During the growth of the stock the basal plate gradually undergoes changes. The parenchyme becomes filled with yolk globules (Plate V. Fig. 49), and the cuticula becomes thick and dark.

Concerning the morphological significance of the basal plate a few words must be said. I regard this as a stolon morphologically equivalent to the stolon of the Pedicellinidæ. In the latter group, as is well known, the individuals are budded from the upper side of a repent cylindrical stolon, which constantly produces new buds at the growing end, and which becomes separated into segments by the formation of transverse dissepiments. There is no such stolon in the adult Urnatella, which is sharply separated from the Pedicellinidæ by this single character. The presence of a stolon in the young stock indicates a derivation from an ancestral condition possessing a stolon in the adult.

If, however, the " stolon " of the young Urnatella stock is homologous with that of the Pedicellinidæ, we ought to find it, sometimes at least, giving rise to more individuals than two, and perhaps becoming segmented. Both of these conditions are occasionally fulfilled. Leidy observed that three, four, or even five stems may arise from a common " basal plate." I have observed only three with certainty. Two cases of this are shown in Plate V. Figs. 48 and 49. In the first of the two cases distinct perforated dissepiments were observed dividing the stolon (basal plate) into three segments, out of each of which a single stalk arose.

6. *Formation of the Individual.*

Recent careful studies on the formation of the individual in other Endoprocta, especially by Seeliger ('89[a]), render a detailed study of this process less necessary. There are a few points concerning the physiological rather more than the morphological features of this process which I have attended to in this case in order to test certain conclusions which I had arrived at from the study of the earliest stages of budding in Ectoprocta.

First, the budding regions are areas of cuboidal cells, with relatively large nuclei and deeply staining plasma. Such a condition is found in both the ectoderm and mesoderm of the proliferating region (Plate VI. Figs. 50, 57). The relative enlargement of the ectodermal cells, and at the same time a bending of the whole layer outward, give rise to the first fundament of the new individual. The musculature of the new individuals is certainly not derived directly from that of the old stalk, for this takes no part in the outbending. Upon the apex of the cylindrical protuberance thus formed the polypide is produced. The details of this process I have not followed.

Secondly, the position and time of origin of the buds arising from the stalk are very definite. They make their appearance in a zone lying in the lower part of the segment (Plate VI. Figs. 50, 58–60), and shortly after the formation of the dissepiment which lies just below.

One of the questions the re-examination of which most interested me was that of the origin of the alimentary tract, since this is stated to arise differently in Endoprocta and Ectoprocta.

In an optical section of the whole bud (Plate VI. Fig. 53), it could be seen that the atrium was connected with the young alimentary tract at the oral end only. The same thing is shown in the series of transverse sections, Figures 54–56, in which the distal (anal) part of the atrial chamber is not confluent with the rudiment of the alimentary tract which touches its floor, Figure 54, but the two organs are confluent at the proximal (oral) part, Figure 56. Figure 52 is from an optical longitudinal section of the bud shown in Figure 53, taken in a plane perpendicular to that of Figure 53. Here the alimentary tract, *st.* (Fig. 52; *ga.* Fig. 53) is being constricted off from the atrium.

Like the young bud, the growing tip of the stolon possesses an ectoderm consisting of large cuboidal cells (Plate VI. Fig. 57). The mesenchymatous tissue also consists of thickly crowded, undifferentiated, and deeply staining cells (Figures 51, 57).

7. *Regeneration.*

Like other Endoprocta, Urnatella has the capacity of regenerating its lost calyces. Leidy ('84, p. 13) had already observed this process, and Potts and I have (as previously mentioned) seen the same thing. Figures 3 and 2 (Plate I.) show some of the phenomena of regeneration. The formation of a new terminal calyx seems to be preceded by the formation of the stalk part of the new terminal individual. This new formation takes place in one of the segments near the distal end of the parent stalk. The terminal dissepiment of the segment, cutting it off from the outside world, is completely closed in its centre by a cuticular plug. This cuticular dissepiment (Fig. 2, *di. sep.* at the left) becomes torn off from the lateral cuticula of the segment along one edge, sometimes, as in the figure, remaining attached at the opposite edge. I have given on Plate I. (Fig. 3) a drawing of such a regenerating stalk before the polypide has budded from its wall. The outer body wall has evidently taken the initiative in the process, and mesenchymatous cells have migrated in. The drawing (Fig. 3) was made from the living animal, and the mesenchymatous cells could be seen changing form like an amoeba. The amoeboid cells also contained highly refractive granules, which I regard as food material. These granules were seen moving about in the cells as the latter changed in form.

One striking feature of the young segment was the presence of two flickering organs, which I now fully believe to be flame cells with their tufts of fused cilia. I have elsewhere ('91, p. 39) called attention to the part played by amoeboid cells in Paludicella on the nutrition of the young buds. I believe that the amoeboid cells here have the same function.

Leidy ('84, p. 13) has suggested that the segments of Urnatella might function as statoblasts to preserve the species during the winter. Of the correctness of this suggestion I have no doubt. The ease with which regeneration occurs from the old segments, and the fact that in stalks in which the calyces have been for a long time lost one sees the cirri of the flame cells still flickering, show that the tissue surrounded by the thick cuticula of the segments has a great capacity for retaining life, and, under favorable conditions, for reproducing lost parts. In their *rôle* as statoblasts, the segments need the yolk stored up in their cells during the summer.

IV. Affinities of Urnatella.

From the frequent opportunity that I have had successfully to compare the organs of Urnatella, even in detail, with those of Pedicellina and allied genera, there remains no doubt in my mind of its close relationship to those forms. Arthropodaria, especially in its segmentation of the stem and the associated budding process, seems most closely to resemble Urnatella. In three points of importance, however, Urnatella differs from other Pedicellinidæ, namely : (1) in the possession of a cloaca (and absence of a brood-sac?) ; (2) in the presence of water or excretory canals in the stem and calyx, — which are so striking that they could hardly have been overlooked if they occurred in other Pedicellinidæ; and (3) in the absence of the stoloniferous type of budding.

As for the last difference, however, I have tried to show that there is a stolon from which the individuals of the Urnatella stock arise, although it is small. Whether this rudimentary condition of the stolon is an ancestral or a degenerate character is doubtful ; I have been inclined to consider it the latter.

In regard to the first difference, I must point out that in the male of Arthropodaria there is a condition resembling that found in Urnatella, for in the former genus (Foettinger, '87, Plate X. Fig. 8) the anus, vas deferens, and excretory tubule open near together.

The second difference concerns a very important set of organs, and if they should be shown to be indeed absent in Arthropodaria Benedeni, it would lead us to conclude that in one respect at least, perhaps owing to physiological needs, Urnatella has retained a more ancestral condition than its near allies.

V. Affinities of the Bryozoa.

There are three prevailing views concerning the relationship of the Bryozoa to other groups. According to one view (most recently and ably defended by Ehlers) they find their nearest allies in the Gephyrea ; according to the second view, they have sprung from the lower worms, — from Rotifer-like ancestors. The third view (that of Hatschek) assumes that Ectoprocta and Endoprocta are in fact not closely related, but that the former should be placed near the Gephyrea, the latter close to the Rotifera.

The reasons for this difference of opinion are not far to seek. Those who have begun their studies with the Ectoprocta, particularly with

their anatomy, have been struck by their resemblance — especially in the possession of a body cavity and of a tentacular corona — to the Gephyrea, and particularly to Phoronis. Those, on the contrary, who have devoted their studies chiefly to the Endoprocta, and especially to the development of that group, have urged the second view. The third view seeks to reconcile the two conflicting theories. I favor the second of the views given above because of certain considerations which follow.

I propose first to show the untenableness of the third view. It would then be nearly sufficient, in deciding between the two remaining views, to show that the Endoprocta are the more primitive group of Bryozoa; but in addition to this, I shall offer positive evidence of derivation of the Bryozoa from the lower worms.

The chief argument for the diphyletic origin of Bryozoa rests on these three important differences between Ectoprocta and Endoprocta: (1) that of the tentacular corona, which includes within it the anus in one case, and leaves it outside in the other ; (2) that of the body cavity, which is absent in one case and present in the other ; and (3) that of the kidney, which is a pronephridium in Endoprocta and (it is alleged) a metanephridium in Ectoprocta.

I have, in an earlier paper ('91[a], p. 103), shown that the difference in relations of the anus to tentacular corona is completely and satisfactorily explained by the study of the development of the polypide, in which the closure of the tentacular corona between mouth and anus is effected only at a relatively late stage.

Concerning the second of these differences, Ehlers ('90, pp. 152, 154) has already well argued that it cannot be so fundamental, since other un-questionably closely allied groups (e. g. Hirudinea and Chætopoda) differ similarly. Moreover, the difference between the " body cavity " of Gym-nolæmata and Endoprocta is one of degree, not of kind, for in both cases we have to do with parenchymatous tissue more or less completely filling the primary body cavity. The existence of spaces in the midst of the parenchyme of Gymnolæmata may be accounted for (following Harmer, '85, p. 64, see also Lang, '88, p. 77) on the physiological ground of the necessity of a space into which the polypides can retract. In Phylac-tolæmata this parenchyme has become, in part, a very definite " coelomic epithelium," although, as I have pointed out ('90, p. 128), showing traces of its parenchymatous origin.

Upon the alleged differences in the kidney, no argument can be based, simply because the existence of an excretory tubule in Ectoprocta is very uncertain, being at present not even probable.

A fourth difference, which I do not remember to have seen mentioned, concerns the position of the sexual glands. In Endoprocta they arise on the polypide and are connected with the atrium by a special duct. In Ectoprocta they arise on some part of the body wall. In all cases, however, they arise from the mesenchymatous tissue, or its equivalent, the cœlomic epithelium. The exact position is not significant, for even within the group of Phylactolæmata we find the testis arising sometimes on the funiculus (Plumatella), sometimes on the body wall (Cristatella), and in neither case at the same place with the ova.

On the other hand, the resemblances between Ectoprocta and Endoprocta are striking : in both a curved alimentary tract, with tentacles of similar histological structure ; in both, an atrium originating in the same manner ; the central nervous system in both alike in position, form, structure, and development ; in both the polypide originating in comparable ways, involving the same problem of the relation of the germ layers to the organs of the bud. Moreover, there must remain unmentioned many minor resemblances which individually are not very significant, but which, occurring together, furnish a most powerful argument to the mind of one studying the animals themselves.

. Hatschek's view seems to me, therefore, untenable, and it remains to inquire whether the Bryozoa have been derived, accompanied by degeneration, from an Annelidan ancestry, through Gephyrean-like forms,[1] or whether they represent a persisting low type. As we have seen, the first hypothesis must be relinquished, if it can be shown that the Endoprocta are the more ancestral type.

In any group of sessile, colonial animals, we should expect the more ancestral type to retain more distinctly its individuality, to possess in a more marked degree features belonging to a free, non-colonial life, and in a less marked degree those belonging to a sessile, colonial one. Thus in its development the group will lose certain characters and gain certain others.[2] A well marked individuality accompanied by a simple

[1] As is well known, Hatschek ('83, p. 69) has long maintained that Phoronis and the Sipunculaceæ have not been derived from Annelids as the Echiurida have, but from unsegmented ancestors; and this view has become very widely accepted. Ehlers, however, seems to adhere to the older view. Whatever the truth may be in regard to this matter, the validity of my argument based on embryology and comparative anatomy concerning the absence of close relationship between Phoronis and Bryozoa is not affected.

[2] Lang ('88) has shown, by an instructive analysis, that in sessile animals locomotor and sense organs, the nervous system, and the musculature tend to degenerate, and that the tentacles and protective coverings become more important.

method of budding (Loxosoma); a relatively poorly developed, incompletely retractile lophophore; a complicated system of sense organs and nerves (Loxosoma); sexual and excretory ducts; a typical larval (trochophore) form, — these distinguish the Endoprocta. On the other hand, the Ectoprocta are marked by a loss of individuality (existence of cœnocœl, Phylactolæmata), by a highly complicated lophophore provided with means for complete retraction, by absence of a complicated nervous system (small ganglion of Gymnolæmata), by absence (?) of sexual and excretory ducts, and by abbreviated larval life (passed within the body of the mother).

Stronger than this argument is the fact that in the development of the tentacular corona and of the alimentary tract — at first without a cœcum — Ectoprocta pass through stages more nearly resembling the adult Endoprocta condition than their own adult condition does.

These facts seem to me to prove, if morphological principles can be relied upon, that Endoprocta are nearer the ancestral form of Bryozoa than Ectoprocta.

Admitting that the Endoprocta are more ancestral than the Ectoprocta, I cannot conceive how any one can maintain a close relationship with Phoronis. For the line connecting mouth and anus is in Endoprocta ventral, while the corresponding line in Phoronis is dorsal, as Caldwell ('83, p. 372) has shown, and the kidney is a metanephridium. These facts far outweigh, in my opinion, similarities in tentacular corona, epistome, and bent alimentary tract.

The absence of a true body cavity, and the existence of a water or excretory system ending in flame cells, point conclusively to an origin of Bryozoa from the lowest worms. For such an excretory system is found elsewhere only in Platyhelminthes, Rotifera, and in a modified form in Nemertines (Bürger, '91). On the other hand, the existence in the stalk of epithelial (in addition to mesenchymatous) muscles looks like an advance beyond Rotifera and Platyhelminthes. But it does not follow that such muscles existed in the ancestors of Endoprocta; they may have been produced by causes similar to those by virtue of which they occur in Nematodes.

Hatschek ('77, p. 528) suggested, and Harmer ('85, p. 11, 35) has since shown, that the ganglion of the Endoprocta is to be regarded as a subœsophageal ganglion. Zelinka's ('91, p. 337) discovery of a subœsophageal ganglion in Rotifers is interesting in this connection, as making more probable the assumption necessary for the preceding view, that the ancestor of Rotifers and Endoprocta possessed such an organ.

One cannot refrain from noticing the similarity in the relations of the "under lip" of Rotifers (Zelinka, '91, Taf. III. Fig. 55) and the epistome of Bryozoa (cf. also the foot of Mollusks).

Zelinka has also shown (p. 397) that in Callidina at an early stage two lateral folds appear on the ventral side of the embryo, enclosing between them the mouth and under lip. These folds extend along about one half of the length of the embryo. Later they become relatively shorter, and finally form the lobes of the wheel organ. They have also precisely the position of the lophophoric ridges of Ectoprocta at an early stage, as I have figured it ('91, Fig. 25), lying on each side of the mouth and ganglion. They have also the same relations as the ridges from which the gill filaments arise in Lamellibranchs. Lankester's ('74, p. 80) view of the homology of the tentacles of Bryozoa and gill filaments of Lamellibranchs is thus strengthened.

Finally, there is between Rotifers and Endoprocta a striking similarity in the position of anus and urogenital ducts, which in Urnatella, as in Rotifers, open into a common cloaca on the suboesophageal aspect between mouth and anus. Such a resemblance is especially striking in footless genera like Asplanchna (which, however, has no anus, cf. Masius, '91, fig. 1) and Hertwigia (L. Plate, '85, Fig. 7), — genera resembling more nearly the ancestral form, since the foot, lying behind the anus, must be considered as a secondarily produced appendage.

To sum up: The embryological as well as the anatomical evidence seems to sustain the view that Bryozoa are closely related to Rotifers, the two groups having sprung from an ancestor which was common to them and Mollusks also ; that after the Rotifer stem had branched off, the common Mollusco-Bryozoan stem produced tentacles on the lateral ridges ; that the two groups then soon separated, the Mollusca to undergo an extensive and complicated development, the Bryozoa to remain at a low level. The chief changes which the Bryozoa have experienced are (1) the acquiring of a body-cavity through the relative decrease in amount of the mesenchyme, that which remains forming an epithelium (Phylactolæmata); (2) the loss (?) of the protonephridia and sexual ducts in Ectoprocta ; (3) the loss of the epistome (Gymnolæmata) ; (4) the loss of the preoral ganglion ; (5) the acquiring of a cœcum (Ectoprocta); (6) the multiplication of methods of reproduction, by regeneration, by budding (without and with stock-formation), by division of stocks, and by statoblasts.

CAMBRIDGE, September 27, 1892.

Summary.

The segmented stem of Urnatella consists of a two-layered cuticula; an outer epithelium (ectoderm) consisting of cells flattened except at the transverse septa and at the distal end of the stalk; and an axial portion consisting of elongated cells, many of which are vacuolated, and surrounding which there is no intercellular substance.   (Pages 4, 5.)

The musculature of the stalk consists of radial sheets of fibrillæ, several of which develop in a single cell.   (Pages 5, 6.)

Many of the vacuolated cells of the stalk end in flame cells like the water or excretory tubules of Platyhelminthes.   (Pages 6, 7.)

Yolk is developed in the cells at the base of the stalk, first as fine intercellular granules, which later fuse, this process being accompanied by cell degeneration.   (Pages 7, 8.)

The lip of the atrium contains a sphincter, and resembles in its relations the "margined thickening" of Ectoprocta.   (Pages 9, 10.)

The epithelium of the tentacles encloses a parenchymatous core.   A pair of muscles is present.   (Page 15.)

The alimentary tract resembles that of the Pedicellinidæ, except that the lower wall of the rectum and the upper wall of the intestine are in close contact.   (Pages 11, 12.)

The nephridial tubules end blindly in flame cells, and open into a cloaca, into which open also anus and the vas deferens.   (Pages 14, 15.)

Two kinds of buds arise from the Urnatella stalk; "branches," which are typically median, and "stolons," typically lateral.   (Page 16.)

The segmentation of the stalk is probably an adaptation to the process of budding, which is accompanied by a greater liability of the wall of the stock to rupture, and therefore by a greater need of separation of the stalk into compartments.   (Page 20.)

In all Endoprocta the oral aspect of the buds is turned towards the centre of proliferation, and in all Bryozoa the aspect in which that end of the alimentary tract which arises from the principal outpocketing of the atrium lies is turned towards the gemmiparous zone.   (Pages 22, 23.)

The youngest stocks found consisted of a stolon bearing two individuals.   This has been derived from the "stolons" of the parent stalk, which habitually become free for the purpose of founding new stocks. (Page 26.)

Urnatella is, structurally, one of the Pedicellinidæ and most nearly resembles Arthropodaria Benedeni.   (Page 30.)

The Bryozoa have probably been derived from Rotifer-like ancestors. (Page 34.)

LITERATURE CITED.

Allman, G. J.

'56.   A Monograph of the Fresh-water Polyzoa.   viii + 119 pp., 11 Pls.
London : Ray Society.

Bürger, O.

'91.   Die Enden des exkretorischen Apparates bei den Nemertinen.   Zeitschr.
f. wiss. Zool., LIII. p. 322.

Caldwell, W. H.

'83.   Preliminary Note on the Structure, Development, and Affinities of
Phoronis.   Proc. Roy. Soc. Lond., XXXIV. p. 371.

'85.   Blastopore, Mesoderm, and Metameric Segmentation.   Quart. Jour.
Micr. Sci., XXV. p. 15.

Davenport, C. B.

'90.   Cristatella : the Origin and Development of the Individual in the Col-
ony.   Bull. Mus. Comp. Zoöl. at Harvard College, XX. No. 4, p. 101.

'91ₐ.   Observations on Budding in Paludicella and some other Bryozoa.   Bull.
Mus. Comp. Zool. at Harvard College, XXII. No. 1, p. 1.

Ehlers, E.

'90.   Zur Kenntniss der Pedicellineen.   Abhandl. königl. Gesellsch. d. Wiss.
zu Göttingen, XXXVI.   200 pp., 5 Taf.

Fœttinger, A.

'87.   Sur l'anatomie des Pédicellines de la côte d'Ostende.   Arch. de Biol.,
VII. p. 299.

Harmer, S. F.

'85.   On the Structure and Development of Loxosoma.   Quart. Jour. Micr.
Sci., XXV. p. 261.

Hatschek, B.

'77.   Embryonalentwicklung und Knospung der Pedicellina echinata.   Zeit-
schr. f. wiss. Zool., XXIX. p. 502.

'83.   Ueber Entwicklung von Sipunculus nudus.   Arbeit. a. d. zool. Inst.
Wien, V. p. 61.

Kraepelin, K.

'92.   Die deutschen Süsswasser-Bryozoen.   II.   Entwickelungsgeschicht-
licher Teil.   Abhandl. der naturwiss. Verein in Hamburg, XII.   67 pp.,
5 Taf.

Lang, A.

'88.   Ueber den Einfluss der festsitzenden Lebensweise auf die Thiere.
Jena, G. Fischer.

Lankester, E. R.
'74. Remarks on the Affinities of Rhabdopleura. Quart. Jour. Micr. Sci., XIV. p. 77.

Leidy, J.
'51. On some American Polyzoa. Proc. Acad. Nat. Sci. Philad., V. p. 320.
'54. On Urnatella gracilis and a new Species of Plumatella. Proc. Acad. Nat. Sci. Philad., VII. p. 191.
'70. [Note on Urnatella.] Proc. Acad. Nat. Sci. Philad. for 1870, p. 100.
'84. Urnatella gracilis, a Fresh-water Polyzoan. Jour. Acad. Nat. Sci. Philad., (2.), IX. p. 5.

Masius, J.
'91. Contribution à l'étude des Rotateurs. Arch. de Biol., X. p. 651.

Nitsche, H.
'69. Beiträge zur Kenntniss der Bryozoen. II. Ueber die Anatomie von Pedicellina echinata. Zeitschr. f. wiss. Zool., XX. p. 1.

Plate, L. H.
'85. Beiträge zur Naturgeschichte der Rotatorien. Jena. Zeitschr., XIX. p. 1.

Seeliger, O.
'89ª. Die ungeschlechtliche Vermehrung der endoprokten Bryozoen. Zeitschr. f. wiss. Zool., XLIX. p. 168.
'90. Bemerkungen zur Knospenentwicklung der Bryozoen. Zeitschr. f. wiss. Zool., L. p. 560.

Stuhlmann, F.
'87. Zur Kenntnis des Ovariums der Aalmutter. Abhandl. naturwiss. Verein in Hamburg, X. 48 pp.

Vigelius, W. J.
'84ª. Ueber Barentsia bulbosa Hincks. Bijdragen en tot de Dierkunde, XI. p. 85.

Zelinka, C.
'91. Studien über Räderthiere. III. Zur Entwicklungsgeschichte der Räderthiere nebst Bemerkungen über ihre Anatomie und Biologie. Zeitschr. f. wiss. Zool., LIII. p. 1.

ANALYTICAL INDEX

TO DAVENPORT '90, '91ª, AND THE PRESENT PAPER.[1]

The Roman numerals refer to these three papers in the order of publication. The Arabic numerals refer to pages. Topics are arranged alphabetically, except under "Groups," where the main divisions are arranged according to an adopted zoölogical system. Under "Organography" letters are placed after certain page numbers to designate the standpoint from which the organ is treated. The letters apply to all the page numbers between them and the next preceding letter. These letters have the following significations: **A**, Anatomy; **F**, Function; **H**, Histology; **O**, Ontogeny; **P**, Phylogeny.

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EXPLANATION OF PLATES.

All figures were drawn with the aid of a camera lucida, from preparations of Urnatella gracilis, unless otherwise stated.

PLATE I.

ABBREVIATIONS.

atr.	Atrium.	*di. ba.*	Basal disk.
cic.	Scar of fallen-off bud.	*di. sep.*	Transverse septum.
cl. flm.	Flame cell.	*gm.*	Bud.
cl. mi.	Migratory cell.	*mu.*	Muscle fibre.
cla.	Cuticula.	*nl.*	Nucleus.
cx.	Calyx.	*pli. crc.*	Circular folds.
cx. rgn.	Regenerating calyx.	*vt. gran.*	Yolk granules.

Fig. 1. Regenerating stalk of Urnatella, viewed as an opaque object. × 96.

" 2. Optical section of the same. × 96.

" 3. Optical section of the distal end of a stalk of Urnatella which is probably about to regenerate, from living animal. × 410.

" 4. Optical section of the proximal urn of the stalk of Urnatella. Showing thick cuticula and yolk granules. × 165.

" 5. Contents of proximal urn, obtained by crushing. Moving cilia were visible. Nuclei in some of the yolk granules. × 320.

" 6. Stock of Urnatella viewed as opaque object. Three stems arising from the basal disk. Buds and regenerating terminal calyces. × 36.

" 7. Optical section of stalk of Urnatella. × 96.

1.

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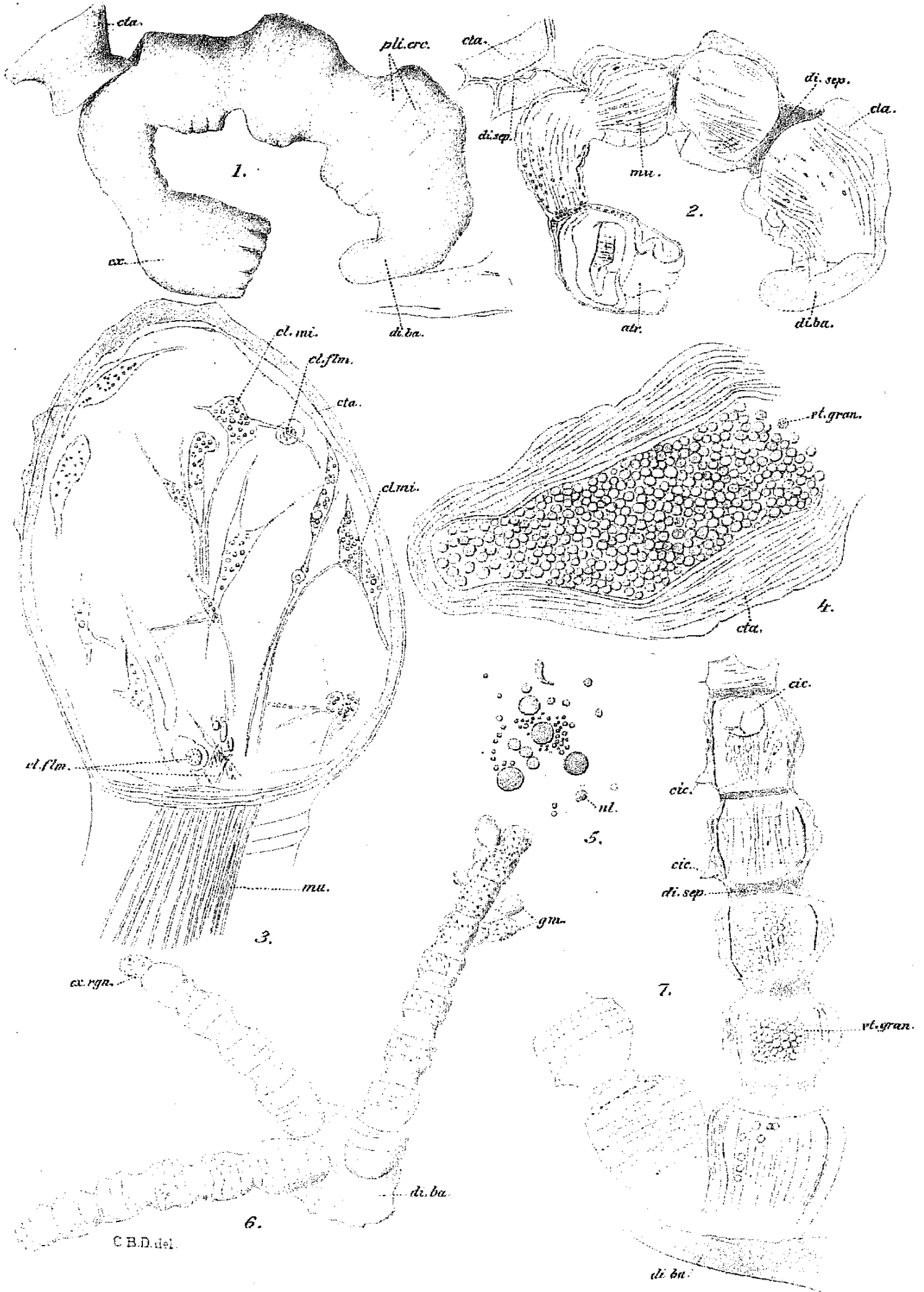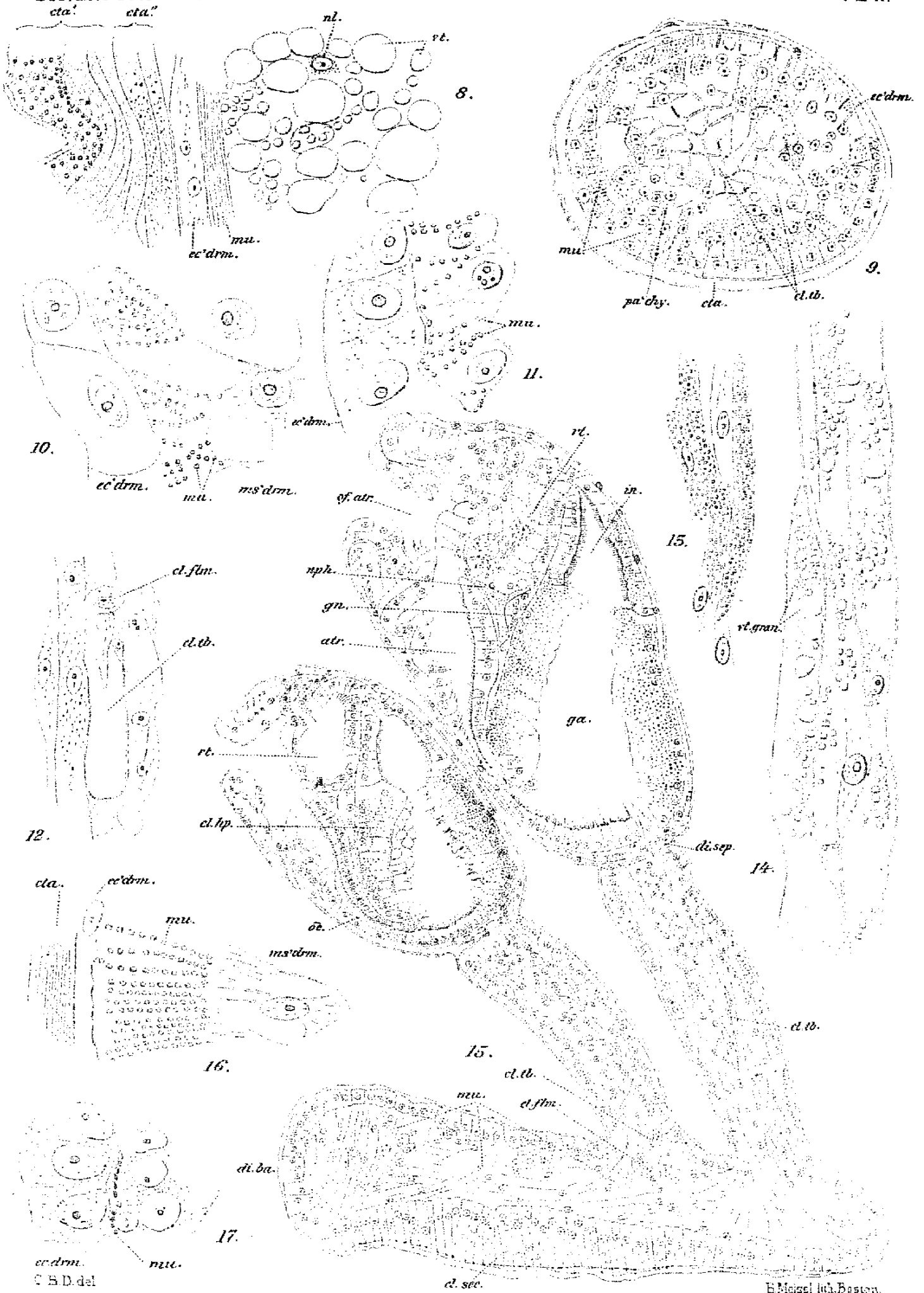
5.

6.

7.

C.B.D. del.

PLATE II.

ABBREVIATIONS.

atr.	Atrium.		*gn.*	Ganglion.
cl. flm.	Flame cell.		*in.*	Intestine.
cl. hp.	Hepatic cells.		*ms'drm.*	Mesoderm.
cl. sec.	Secreting cells.		*mu.*	Muscle fibre.
cl. tb.	Tubular cells.		*nl.*	Nucleus.
cta.	Cuticula.		*nph.*	Nephridium.
cta.'	Outer cuticula.		*œ.*	Œsophagus.
cta.''	Inner "		*of. atr.*	Atrial opening.
di. ba.	Basal disk.		*pa'chy.*	Parenchyme.
di. sep.	Dissepiment.		*rt.*	Rectum.
ec'drm.	Ectoderm.		*vt.* or	⎱ Yolk granules.
ga.	Stomach.		*vt. gran.*	⎰

Fig. 8. Longitudinal section through proximal part of stalk of Urnatella. Third stage in the formation of yolk granules. × 610.

" 9. Cross section through distal segment of stalk, showing ectoderm and parenchymatous tissue inside. × 405.

" 10. Third stage in the development of the stalk muscles. Zeiss, $\frac{1}{12}$ oil immers., Oc. 2. × 1350.

" 11. Second stage in the development of the stalk muscles. × 1350.

" 12. Termination of excretory tubule of stalk in flame cell. The position of the calyx is above. × 305.

" 13. First stage in development of yolk in stalk. × 610.

" 14. Second stage in development of yolk in stalk. × 610.

" 15. Median section through young stalk (age of Fig. 31 in Plate V.). × 165.

" 16. Fourth stage in the development of the stalk musculature. × 1350.

" 17. First stage in the development of the stalk musculature. × 1350.